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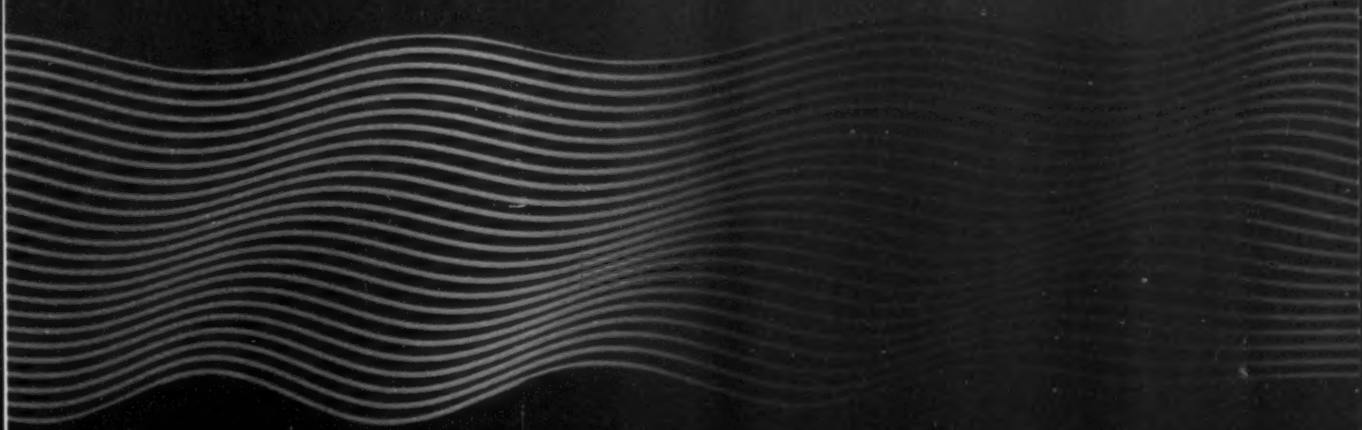

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Rapid recovery of exhausted adult coho salmon after commercial capture by troll fishing

Anthony P. Farrell, Patricia E. Gallaugher, and Richard Routledge

Abstract: To reduce mortality in the by-catch of commercial salmon fisheries, techniques are being explored to revive fish before live release and improve survival. By measuring blood and muscle variables, we demonstrated that capture of coho salmon (*Oncorhynchus kisutch*) by commercial trolling methods resulted in severe exhaustion and stress, e.g., muscle lactate reached 46.1 $mmol \cdot kg^{-1}$ while muscle phosphocreatine (PCr) decreased to 6.1 $mmol \cdot kg^{-1}$. Nevertheless, coho salmon recovered rapidly by swimming in a cage alongside the vessel while fishing activity continued. In particular, there were significant increases in muscle glycogen and PCr levels, and a decrease in muscle lactate after two hours. Notably, and in contrast to when exhausted fish are held stationary during recovery, plasma lactate remained low (<4 $mmol \cdot L^{-1}$) during recovery, a phenomenon observed in earlier laboratory studies with rainbow trout (*Oncorhynchus mykiss*). There was no postcapture delayed mortality after 24 h. Therefore, we have established that postexhaustion activity promotes a rapid recovery in wild salmon and this result might find application in nonretention commercial and recreational fishing.

Résumé : On est actuellement à la recherche de techniques pour diminuer la mortalité des prises accessoires dans la pêche commerciale au saumon, en réanimant les poissons avant de les libérer pour augmenter leur survie. La mesure des variables du sang et des muscles nous a permis de démontrer que la capture des Saumons coho (*Onchorhynchus kisutch*) par les méthodes commerciales de pêche à la traîne produit un épuisement et un stress graves; e.g., la concentration de lactate dans le muscle atteint 46,1 $mmol \cdot kg^{-1}$, alors que celle de la phosphocréatine du muscle est réduite à 6,1 $mmol \cdot kg^{-1}$. Néanmoins, les Saumons coho se sont rétablis rapidement en nageant dans une cage fixée sur le côté du navire, alors que la pêche se poursuivait. Il y avait, en particulier, des augmentations significatives des concentrations de glycogène et de phosphocréatine dans les muscles et une réduction du lactate musculaire après deux heures. Contrairement aux poissons épuisés gardés au repos durant la récupération, les poissons actifs ont maintenu des concentrations de lactate plasmatique basses (<4 $mmol \cdot L^{-1}$) durant la récupération, un phénomène observé antérieurement en laboratoire chez la Truite arc-en-ciel (*Oncorhynchus mykiss*). Il n'y avait pas de mortalité différée 24 h après la capture. Nous avons donc conclu qu'une activité après l'épuisement favorise une récupération rapide chez les saumons sauvages; nos résultats peuvent sans doute s'appliquer à la gestion des poissons qui ne sont pas retenus dans les pêches commerciales et sportives.

[Traduit par la Rédaction]

Introduction

Commercial fisheries worldwide are estimated to discard 38% of fish caught, i.e., they are thrown back with no attempt at revival (Alverson et al. 1994). Of those fish not already dead, many may either suffer postcapture delayed mortality, be captured by predators, or because of their weakened state, be recaptured by commercial fishers. The Canadian selective fishing policy, instituted in 1998 to conserve certain salmon stocks that are at low levels, includes revival and nonretention of nontarget coho salmon (*Oncorhynchus kisutch*).

In collaboration with Fisheries and Oceans Canada, we have been assessing coho salmon revival on board commercial salmon fishing vessels in British Columbia (Farrell et al. 2000, 2001; S. Buchanan, A.P. Farrell, J. Fraser, P.E. Gallaugher, R. Joy, and R. Routledge, unpublished data). "Blue box" revival tanks are presently used on board gillnet vessels because they can promote low 24-h delayed mortality rates (Farrell et al. 2000), even though they were rather ineffective at promoting physiological recovery on board gillnet, seine, and troll vessels, in that there was no significant recovery of muscle concentrations of phosphocreatine (PCr), glycogen, and lactate after 1 h. A modified revival

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tank in which there is a laminar flow of water over the fish (a Fraser box) is accepted as an improvement over the blue box because when used in conjunction with modified gillnet gear and methods, the Fraser box promotes significant recovery of muscle PCr and lactate concentrations in 1 h and restores swimming performance, as well as keeping 24-h delayed mortality rates low (Farrell et al. 2001; S. Buchanan, A.P. Farrell, J. Fraser, P.E. Gallaugher, R. Joy, and R. Routledge, unpublished data). The present study reports on another successful revival technique for coho salmon. Troll-caught fish were transferred to and revived in a submerged cage attached to the side of the vessel while fishing activity continued. Recovery in a submerged cage had an additional benefit over the blue box and the Fraser box of maintaining plasma lactate at very low levels during recovery.

Materials and methods

Coho salmon were caught with commercial troll gear using barbless hooks by the vessel Sherry Shan in Barkley Sound, B.C., Canada during 1998 and 1999. Fish were either sacrificed for tissue sampling immediately as they reached the surface or quickly transferred without air exposure to an aluminum-framed cage attached to the side of the troll vessel. The cage (~1.22 m deep) was almost completely submerged and had light canvas sides and a see-through mesh top. A hinged door on top of the cage swung open to allow fish to be flicked off of the hook and into the cage. Fishing activities continued with the vessel moving at a variable speed of 1–2 knots. Therefore, to keep pace with the vessel, the fish (60–80 cm in length) swam at speeds of ~0.75–1.5 fish body lengths$\cdot$s^{-1} (bl$\cdot$s^{-1}). After a recovery period of about 2 h, fish were either removed from the cage with a dipnet for tissue sampling or transferred to a commercial netpen (12 m × 12 m × 12 m) to complete a 24-h recovery. For transfer, the cage was detached from the fishing vessel and the back end was slid into the netpen. A vertical panel in the back end of the cage was lifted and the front end was raised, allowing the fish to swim into the netpen. Water temperature ranged between 12°C and 16°C.

Blood and muscle samples were taken to assess physiological status. Tissue collection and analytical techniques followed those fully described in Farrell et al. (2000, 2001). Briefly, fish were stunned at the water level by a blow to the skull. Then a muscle sample from a location below and slightly anterior to the dorsal fin was quickly (in <35 s) removed and frozen between precooled metal tongs. The frozen tissue was placed in aluminum foil and stored on dry ice. Directly following the muscle biopsy, blood was drawn by caudal puncture into a 3-mL heparinized vacutainer and two heparinized hematocrit tubes were filled immediately from the blood sample. Plasma aliquots were frozen on dry ice. Skeletal muscle and plasma samples were subsequently stored at –80°C prior to analysis in the laboratory. Plasma lactate and glucose concentrations were measured using a YSI 2300 STAT Plus glucose and lactate analyzer (YSI Inc., Yellow Springs, Ohio). Plasma cortisol was measured in duplicate after suitable dilution using a commercial ELISA kit (enzyme-linked immunosorbent assay, Neogen Co., Lexington, Ky.). Plasma chloride concentrations were measured in duplicate using a model 4425000 digital chloridometer (Haake Buchler Instruments, Saddle Brook, N.J.). Concentrations of plasma sodium and potassium ions were measured using a model 510 Turner flame photometer (Palo Alto, Calif.). Plasma osmolality was measured using a model 5500 vapour pressure meter (Vapro, Wescor, Logan, Utah). Muscle glucose and lactate concentrations were determined with perchloric acid extracts using the glucose and lactate analyzer, and glycogen was determined as glucosyl units after digestion with amyloglucosidase. Muscle PCr and adenosine triphosphate (ATP) concentrations were determined enzymatically. All procedures were approved by the Simon Fraser University Animal Care Committee in accordance with the Canadian Council on Animal Care.

Results and discussion

Analysis of plasma and skeletal muscle samples clearly showed that coho salmon were severely stressed and metabolically exhausted immediately after capture (Fig. 1). Importantly, muscle lactate (46.1 mmol$\cdot$kg^{-1}) was ~40% higher than that observed in exhausted rainbow trout (*Oncorhynchus mykiss*) in laboratory studies (Milligan 1996; Kieffer 2000; Milligan et al. 2000) and similar to the levels observed in angled wild Atlantic salmon (*Salmo salar*) (Booth et al. 1995).

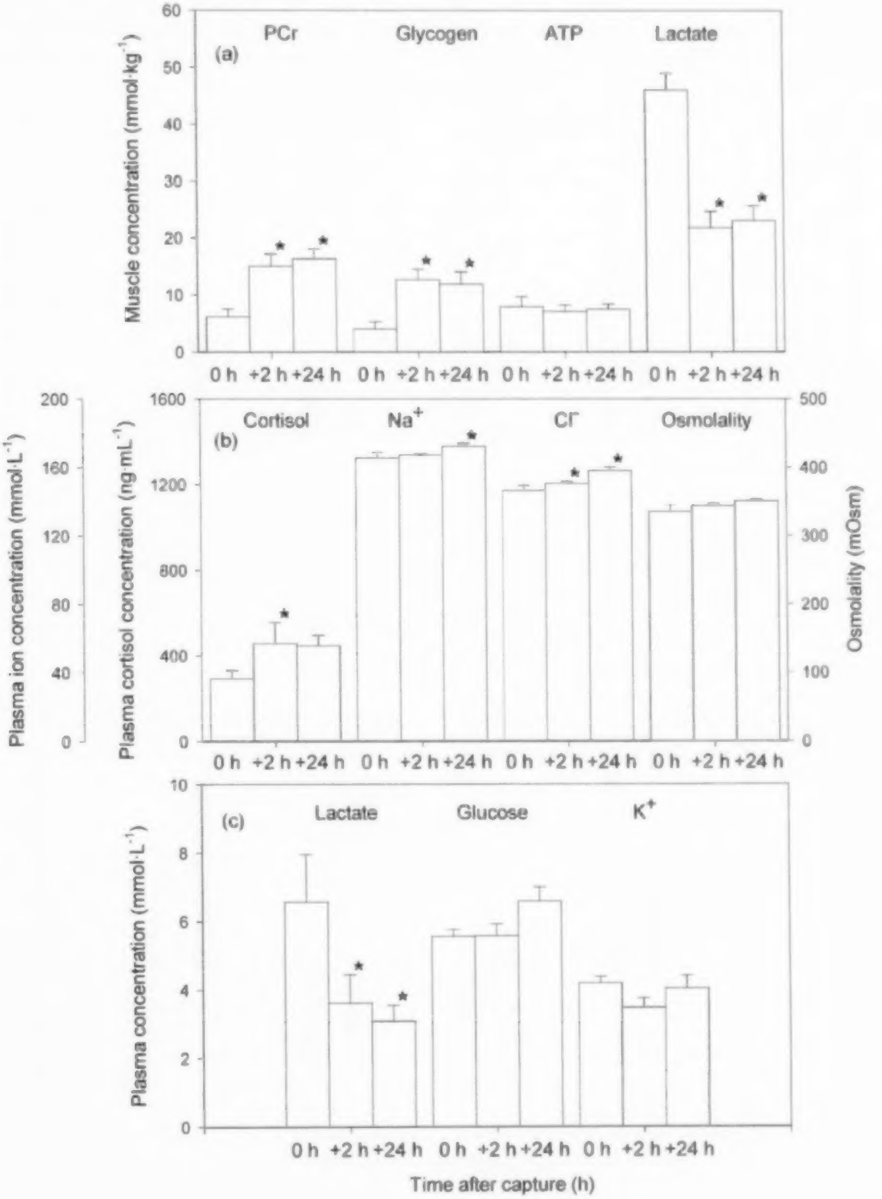
Despite being severely exhausted, coho salmon showed significant metabolic recovery after a 2-h period while swimming alongside the fishing vessel (Fig. 1). Specifically, muscle glycogen increased threefold (from 4.0 to 12.7 mmol$\cdot$kg^{-1}), muscle PCr increased more than twofold (from 6.1 to 15.0 mmol$\cdot$kg^{-1}), and muscle lactate decreased twofold (from 46.1 to 21.2 mmol$\cdot$kg^{-1}) (Fig. 1). Plasma lactate decreased significantly to 3.6 ± 0.5 from 6.6 ± 1.4 mmol$\cdot$L^{-1}. This result contrasted with our earlier work (Farrell et al. 2000, 2001), where plasma lactate increased to about 20 mmol$\cdot$L^{-1} during revival. Plasma cortisol and chloride concentrations increased significantly (Fig. 1).

These findings clearly show that wild adult salmon captured by commercial troll gear can be revived while the fishing vessel continues its fishing activity at sea. Consequently, a cage beside a troll fishing vessel, similar to a Fraser box on board a gillnet vessel (Farrell et al. 2001), provides an effective means to promote physiological recovery of commercially caught coho salmon. The submerged cage offered an advantage over the Fraser box of keeping the plasma lactate concentration low during recovery. By allowing the fish to recover muscle metabolites before release, we anticipate that fish are better able to avoid predators than if they were released directly to the sea in an exhausted state. There might be an added benefit of reducing delayed mortality, but this would be hard to verify experimentally.

Revived fish ($N = 14$ for 2-h recovery; $N = 14$ for 24-h recovery) showed no postcapture delayed mortality after 24 h. This compares very favorably with the delayed mortality rates of ~2% with both the blue box and the Fraser box. With the exception of plasma sodium, the physiological profiles of the plasma and muscle tissue were essentially the same in fish sampled after 24-h and 2-h recovery periods (Fig. 1). By using a dipnet for sampling we may have underestimated the recovery of variables such as muscle PCr, lactate, and glycogen because of fish activity. Also, holding adult salmon in large pens created additional difficulties in obtaining fish without altering their physiological status through activity.

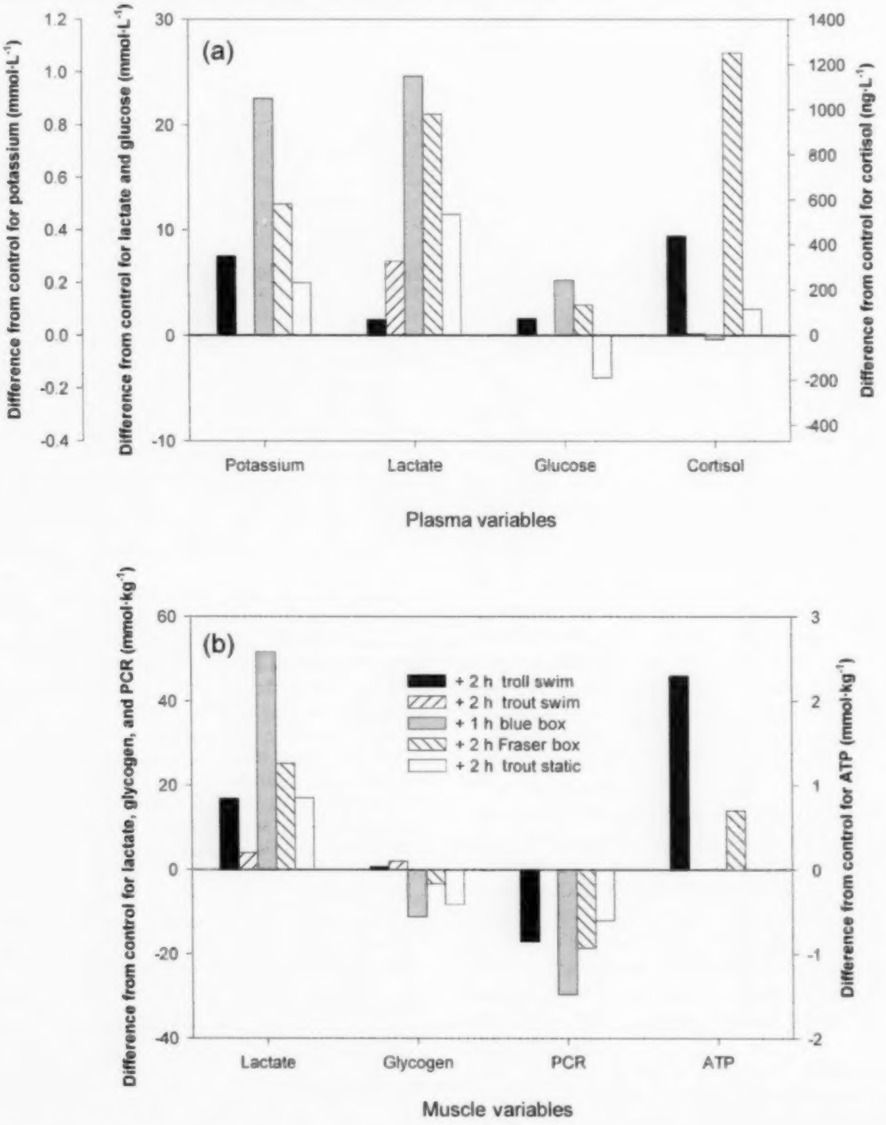
It was not possible to obtain samples from fully rested adult coho salmon on board a commercial vessel, so an evaluation of the extent of the physiological recovery depends on comparisons with other studies. Also, a comprehensive literature review of variables in connection with the Fraser box was published earlier (Farrell et al. 2001). Therefore, rather than

Fig. 1. (*a*) Physiological status of skeletal muscle and (*b*, *c*) plasma in mature wild coho salmon (*Oncorhynchus kisutch*) sampled after capture by commercial troll fishing methods. Sampling was performed immediately after capture (0 h), after a 2-h recovery period while swimming in a cage beside the fishing vessel (+2 h), and after completing a 24-h recovery in a large netpen (+24 h). Hematocrit (39.8 ± 1.5%; $N = 41$) and muscle glucose (1.30 ± 0.16 mmol·kg^{-1}; $N = 38$) were also measured. Mean values are presented for N = 11 to 14 fish, except the ATP value for 0 h where $N = 4$. The standard error of the mean is indicated by the vertical line. Statistically significant differences ($P < 0.05$) from the initial samples are indicated by an asterisk. Statistical tests for differences were done through an analysis of variance (JMP, SAS Institute Inc., Cary, N.C.) with a 5% significance level. All analyses were followed by appropriate multiple comparison tests to determine which means were significantly different (with Tukey or Bonferroni adjustments to reduce the experimentwise error rate to at most 5%).



repeat this comparison, we have compared the results of five recovery methods graphically; three methods involved commercially caught adult coho salmon and two methods involved laboratory studies with rainbow trout (Fig. 2). For this comparison, and where possible for each revival method, we have presented the absolute difference of the recovered vari-

Fig. 2. (*a*) Absolute differences of plasma variables and (*b*) muscle variables from a control value for various methods of reviving salmonids after exhaustive activity. The smaller the absolute difference from the control values (based on average resting values for rainbow trout; Milligan 1996), the smaller the metabolic disturbance remaining for that particular method. From left to right, the fish revival methods were as follows: the present study in which commercially caught wild coho salmon were sampled after swimming for 2 h beside a troll fishing vessel (solid bar, + 2 h troll swim; 12–16°C); rainbow trout sampled 2 h after being chased to exhaustion in a laboratory and allowed to swim moderately during the recovery period (hatched bar, + 2 h trout swim; 12–16°C; Milligan et al. 2000) (values for plasma potassium and glucose and muscle PCr and ATP were unavailable); commercially caught wild coho salmon that were sampled after being revived for 1 h in a blue box on board a fishing vessel (shaded bar, + 1 h blue box; 12–19°C; Farrell et al. 2000) (muscle ATP value unavailable); commercially caught wild coho salmon that were sampled after being revived for 2 h in a Fraser box on board a gillnet fishing vessel (hatched bar, + 2 h Fraser box; 12–16°C; Farrell et al. 2001) (muscle ATP value unavailable); rainbow trout sampled 2 h after being chased to exhaustion in a laboratory and held stationary in a recovery box (open bar, + 2 h trout static; 12–16°C; Milligan 1996; Milligan et al. 2000; C.L. Milligan, Department of Zoology, University of Western Ontario, London, Ont., personal communication) (muscle ATP value unavailable).



able from an average resting value obtained for rainbow trout (Milligan 1996). Ideally, the smaller the absolute difference, the better the recovery. (Note: comparisons could not be made among ionic and osmotic variables because this would involve a comparison between freshwater and saltwater fish.) The temperature ranges of the five studies overlapped, but we cannot exclude temperature differences between experiments as a possible confounding factor in the comparison of recovery methods. We note that the rates of recovery of muscle lactate, glycogen, and ATP are all temperature dependent, while peak muscle lactate and rate of recovery of PCr are independent of temperature (Kieffer 2000).

The comparison presented in Fig. 2 shows that, compared with coho salmon revival in a blue box, physiological recovery was much better when coho salmon recovered either while swimming in a cage or when placed in a Fraser box. Only a 1-h recovery period was examined earlier with the blue box and this complicates the comparison with the present study where only a 2-h recovery was examined. Even so, the physiological recovery observed after 1 h with a Fraser box was not observed with the blue box after 1 h (e.g., muscle lactate was 53.9 $\text{mmol}\cdot\text{kg}^{-1}$ for a blue box compared with 39.9 $\text{mmol}\cdot\text{kg}^{-1}$ for the Fraser box, and muscle PCr was 2.5 $\text{mmol}\cdot\text{kg}^{-1}$ for the blue box compared with 12.2 $\text{mmol}\cdot\text{kg}^{-1}$ for the Fraser box), thus the differences we note are unlikely to be a consequence of a longer recovery period. The blue box also performed more poorly in reviving asphyxiated fish (a >50% delayed mortality rate versus a <7% mortality rate for the Fraser box) (Farrell et al. 2001). Thus, when compared with the blue box recovery method, coho salmon were revived faster, to a greater extent, and with lower delayed mortality rates using both a Fraser box on board a gillnet vessel and caged fish alongside a troll vessel.

Although commercially caught coho salmon showed greater muscle lactate levels than rainbow trout in laboratory experiments, coho salmon held in a cage alongside a troll vessel could recover certain metabolic variables to the same extent as rainbow trout (Fig. 2). In fact, plasma lactate remained lower in swimming coho salmon than in static rainbow trout. Nonetheless, commercially caught coho remain severely stressed during recovery because cortisol levels were elevated to a much greater degree.

Figure 2 shows that coho salmon swimming in a cage alongside a troll vessel recovered as well as or better than coho salmon held for 2 h in a Fraser box. Besides enhanced recovery of muscle metabolites there were lower levels for plasma lactate and cortisol for swimming coho salmon (Fig. 2) as well as 0% versus 2.3% delayed mortality after 24 h (Farrell et al. 2001). We believe that an enhanced recovery compared with the Fraser box relates directly to moderate swimming activity during recovery, notwithstanding the important differences in capture methods between the two studies. This conclusion is consistent with a recent laboratory study on rainbow trout (Milligan et al. 2000) in which moderate continuous swimming activity (0.9 $\text{bl}\cdot\text{s}^{-1}$ in a swimming flume) promoted a threefold faster recovery in rainbow trout (Fig. 2). Although we could not control swimming speed, we estimate that the coho salmon swam at a speed (0.75–1.5 $\text{bl}\cdot\text{s}^{-1}$) comparable to that used earlier with rainbow trout. Furthermore, we can now identify two physiological characteristics shared by fish that swim during their recovery. First, plasma lactate remains very low (<4 $\text{mmol}\cdot\text{L}^{-1}$ in this study; <5 $\text{mmol}\cdot\text{L}^{-1}$ for rainbow trout; <4 $\text{mmol}\cdot\text{L}^{-1}$ for sockeye salmon (*Oncorhynchus nerka*): Farrell et al. 1998) compared with stationary fish (10–15 $\text{mmol}\cdot\text{L}^{-1}$ for rainbow trout and 24.6 $\text{mmol}\cdot\text{L}^{-1}$ for coho salmon; Fig. 2). Second, plasma cortisol levels remain lower (Fig. 2). Although absolute plasma cortisol levels were much higher in coho salmon than in rainbow trout (perhaps as a result of the greater degree of initial stress or because mature Pacific salmon can have much higher cortisol levels), plasma cortisol did not increase nearly as much in swimming versus stationary coho salmon (Fig. 2). Thus, moderate postexercise activity, the equivalent of a "cool-down" period for ectothermic fish, appears to have substantial benefits to the recovery process in salmonids and brings into doubt the longstanding belief that metabolic recovery in severely exhausted fish is necessarily prolonged (e.g., Black 1957; Dobson and Hochachka 1987; Milligan 1996).

An association was made many years ago between elevated plasma lactate levels in exhausted fish and delayed mortality. Subsequently, Wardle (1978) showed that an injection of adrenaline in exhausted plaice (*Pleuronectes platessa*) reduced the appearance of lactate in the plasma and decreased the occurrence of delayed mortality. In the present study, we provided a simpler means of getting the same results. Mild exercise post-exhaustion appears to be the answer to reducing lactate release into the plasma and preventing delayed mortality in salmon.

The exact mechanisms that keep plasma lactate and cortisol low and prevent postcapture delayed mortality are unresolved at this time but have been discussed by Milligan et al. (2000), who suggested a relationship between the plasma cortisol and lactate dynamics. Interestingly, swimming rainbow trout recovered muscle lactate to a lower level (~10 $\text{mmol}\cdot\text{kg}^{-1}$) than did coho salmon (21.2 $\text{mmol}\cdot\text{kg}^{-1}$) and with a lower plasma cortisol level (Fig. 2). This difference again may reflect a linkage between plasma cortisol and lactate dynamics, but we cannot exclude the confounding effect of dipnetting fish in open ocean conditions and taking samples without the aid of anesthesia or cannulation. Although the higher muscle lactate load in coho salmon could have been a factor, with the intramuscular conversion of lactate back to glycogen being a rate-limiting process, the muscle lactate load in both studies decreased by 21–25 $\text{mmol}\cdot\text{kg}^{-1}$ during a 2-h recovery period (from 46 to 21 $\text{mmol}\cdot\text{kg}^{-1}$ versus from 32 to 10 $\text{mmol}\cdot\text{kg}^{-1}$).

In summary, revival of commercially caught nontarget coho salmon prior to release could yield dividends for fish conservation. Consideration, however, must be given to the type of recovery conditions, because they can clearly influence the rate of recovery. We have established that moderate activity promotes rapid recovery of exhausted wild salmon and hope that this result finds application in nonretention commercial and recreation fishing. The absence of delayed mortality after 24 h in the present study is an important new finding because the commercial Pacific troll fishing fleet is currently assigned a mortality rate of 25% for coho salmon by-catch, which is based, in part, on earlier scientific studies that reported delayed mortality rates of 34–52% for coho and 40–80% for chinook salmon (*Oncorhynchus tshawytscha*) from troll fishing (Parker et al. 1959). Armed with this knowledge, both recreational and commercial fishers should be encouraged to further develop methods that optimize recovery of their by-catch prior to release, thereby increasing the chances of fish survival. Furthermore, if future work can demonstrate that this type of rapid recovery is associated with a restored swimming and migratory ability and without impairment of reproductive potential, major progress will accrue for future salmon conservation efforts.

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Multiyear homing of Atlantic cod to a spawning ground

D. Robichaud and G.A. Rose

Abstract: Long-term sonar transmitting tags were implanted in 27 female and 21 male cod (*Gadus morhua*) at the Bar Haven spawning ground in Placentia Bay, Newfoundland, in April 1998. Two thirds of tagged fish were relocated. All relocations during the 1999 and 2000 spawning seasons were within 10 km of the tagging site, the majority being within a few hundred metres. No tagged fish were relocated at other spawning grounds or elsewhere in the bay during the spawning season. Outside the spawning season, several tagged fish were relocated in other parts of the bay at ranges of a few kilometres to 110 km from the tagging site, as were 13 of 15 fishery returns (2 returns from several hundred kilometres outside the bay). Homing rates in 1999 and 2000 were 39% and 53%, respectively, after adjustments for tag loss, mortality, misreporting, and relocation efficiency based on returns from a sea-bed beacon tag left at the Bar Haven grounds. Multiyear homing was observed in 26% of cod. This study provides the first direct evidence that cod undertaking long-distance feeding migrations may home to a specific spawning ground in consecutive years, and a hypothesis for the slow recolonisation rates observed in North Atlantic cod stocks.

Résumé : Des émetteurs sonar de longue durée ont été implantés chez 27 femelles et 21 mâles de Morues franches (*Gadus morhua*) sur la frayère de Bar Haven, dans la baie de Placentia à Terre-Neuve, en avril 1998. Deux-tiers des poissons marqués ont été retracés. Toutes les signalisations durant les périodes de fraye de 1999 et de 2000 se sont produites à moins de 10 km du point de relâchement et la majorité à une distance de quelques centaines de mètres. Aucun poisson marqué n'a été signalé sur d'autres frayères ou ailleurs dans la baie durant la période de fraye. En dehors de la période de fraye, plusieurs poissons ont été retrouvés à divers sites dans la baie, de quelques kilomètres à 110 km du point de relâchement; il en est de même de 13 des 15 poissons retournés par les pêcheurs (2 avaient été capturés à plusieurs centaines de km de la baie). Les taux de retour ont été estimés à 39 % en 1999 et à 53 % en 2000, une fois les corrections faites pour les pertes d'émetteurs, la mortalité, les signalisations erronées et l'efficacité de la resignalisation (basée sur les émissions d'une balise émettrice ancrée sur le fond à la frayère de Bar Haven). Vingt-six pour cent des morues ont effectué un retour sur plus de 1 année. Notre étude fournit donc pour la première fois des données qui indiquent que des morues qui entreprennent des migrations de longue distance pour s'alimenter peuvent retourner sur un site particulier de fraye plusieurs années de suite. Nous proposons aussi une hypothèse pour expliquer le taux réduit de recolonisation observé dans les stocks de morues de l'Atlantique nord.

[Traduit par la Rédaction]

Introduction

Stock structure underpins the spatial and biological rationale for assessment and management of most commercial fisheries and implies a degree of segregation among stocks during spawning. Segregation can occur if individuals show fidelity to spawning grounds adopted or formed at first maturity (spawning-group fidelity) or if they spawn with their natal groups (philopatry). Homing to spawning grounds, philopatric or otherwise, is well known in diadromous fishes (e.g., Groot and Margolis 1991) and has also been observed in freshwater and coral reef fishes (Papi 1992). However, in more broadly distributed marine broadcast spawners, philopatry and homing to spawning grounds have remained largely speculative.

Atlantic cod (*Gadus morhua*) is a continental shelf broadcast spawner that typically spawns in large aggregations at specific locations throughout its North Atlantic range (Brander 1994). Tagging studies have led to speculation that cod may home to the same spawning area, at times over long distances, year after year (Godø 1984; Jónsson 1996; Green and Wroblewski 2000). However, these studies remain inconclusive because only single release and capture points could be determined, or only a single year of study was conducted.

Recent developments in the miniaturization of long-life acoustic transmitters enable fish to be tracked for periods of years and repeatedly relocated. Our goal was to determine the degree of multiyear fidelity of cod to a major spawning ground in Newfoundland waters. We used tags designed to transmit individually coded signals over three spawning seasons, and monitored the spawning ground during the spawning seasons of 1998, 1999, and 2000.

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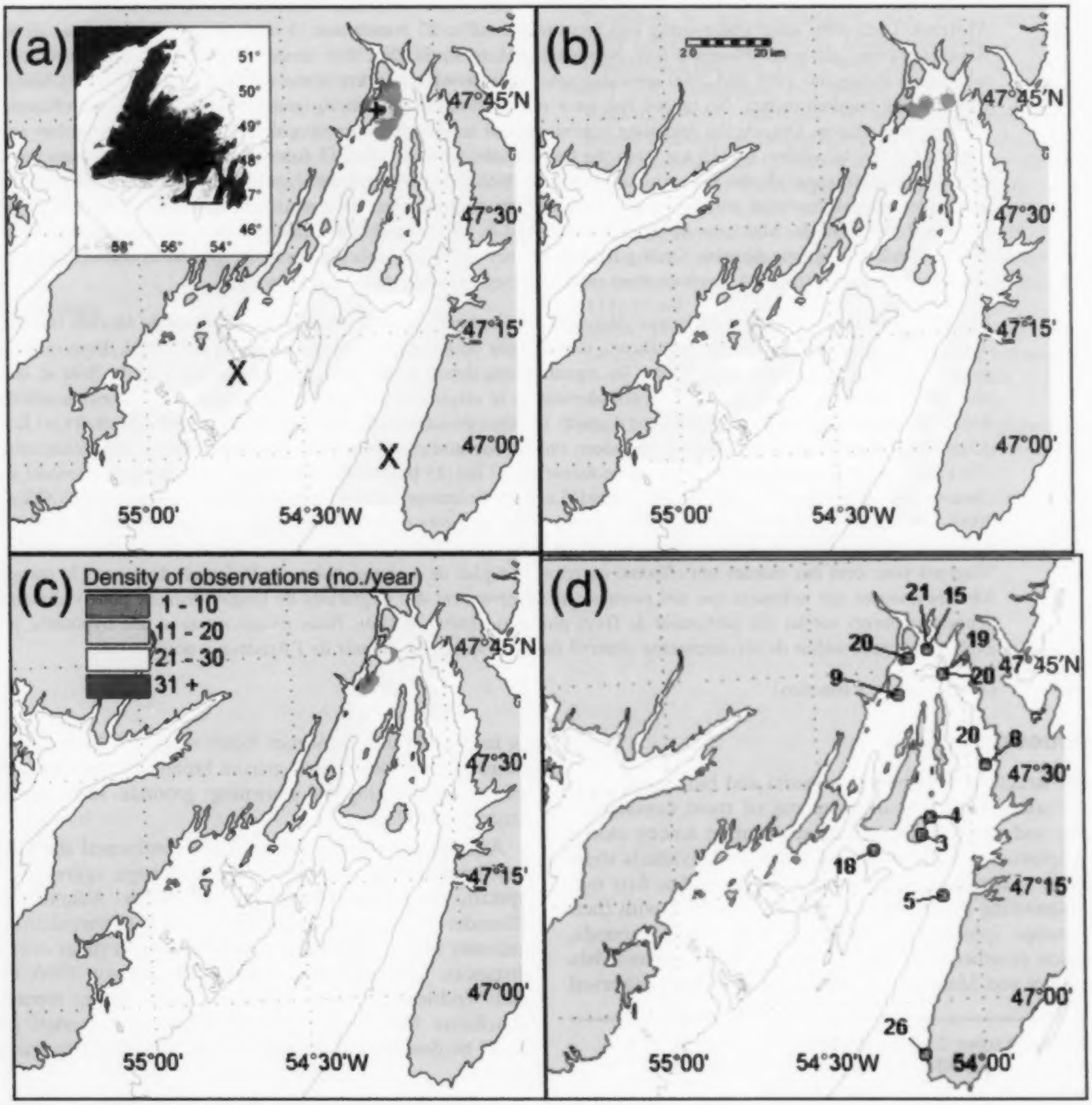
Fig. 1. (*a*–*c*) Density of fish observations (number of relocations over the year (no./year)) in Placentia Bay, Newfoundland, Canada, during three consecutive spawning seasons: (*a*) 1998, (*b*) 1999, (*c*) 2000. Pink areas are the locations monitored during telemetric surveys. Shadings indicate the density of observations (note that the density of observations increases with the number of fish relocated in the same place). In (*a*), + marks the spawning ground where the fish were tagged, and X marks the other known spawning grounds in Placentia Bay. Inset in (*a*) is the island of Newfoundland, with a box showing the location of the Placentia Bay study area. (*d*) Distribution of fishery-returned transmitter catch locations. Numbers indicate months at liberty. The distribution agrees with the known migration pathway of Bar Haven cod into and out of Placentia Bay (Lawson and Rose 2000). No fishery recaptures occurred during spawning season (March to May) when the fishery was restricted. Not shown: one recapture in Conception Bay (47°40′N, 53°00′W, September 1998), and one on St. Pierre Bank (45°05′N, 55°10′W, February 2000).


(a)
51°
50°
49°
48°
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+
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47°45′N
47°30′
47°15′
47°00′
55°00′
54°30′W
(b)
20
20 km
47°45′N
47°30′
47°15′
47°00′
55°00′
54°30′W
(c)
Density of observations (no./year)
1 - 10
11 - 20
21 - 30
31 +
47°45′N
47°30′
47°15′
47°00′
55°00′
54°30′W
(d)
21
15
20
19
9
20
20
8
4
3
18
5
26
47°45′N
47°30′
47°15′
47°00′
55°00′
54°30′W
54°00′

Methods

Study site

The Bar Haven spawning ground (Fig. 1) is located in Placentia Bay, Newfoundland (NAFO Subdivision 3Ps), and is the best known and used ground of the largest contemporary stock in Newfoundland waters (e.g., Lawson and Rose 2000).

Tagging

In April 1998, spawning cod aggregations were located acoustically at Bar Haven. Fish were caught on feather hooks. Larger individuals (>60 cm) thought to be in spawning condition were held in flow-through tanks and sexed by cannulation. For each fish, an individually coded ultrasonic transmitter (Lotek model CAFT16-2, Lotek Wireless Inc., 114 Cabot St., St. John's, NF A1C 1Z8, Canada; 82 mm long, 16 mm diameter; 35.9 g in air, 18.1 g in water; 66 kHz and 76 kHz for males and females, respectively) was surgically implanted into the peritoneal cavity, and an external spaghetti tag was secured adjacent to the first dorsal fin. Tagged fish were held for up to 10 h, and those that appeared to be robust and in excellent condition (only a few were not) were released where caught. In total, 48 cod, including 27 females (lengths 64–87 cm) and 21 males (lengths 67–88 cm), were released. To avoid observing a period of potentially abnormal behaviour after surgery we waited 15 days after tagging before beginning the first telemetric survey.

Telemetry surveys

Fish were monitored in the spring spawning seasons of 1998, 1999, and 2000 using an acoustic receiver (Lotek model SRX-400) and omnidirectional hydrophone (Lotek model LHP-1). Each transmitter emitted a unique coded signal every 5 s. Relocation efficiency, or probability of relocating a tag present in the survey area, was defined as the proportion of surveys in which a beacon tag (a transmitter left on bottom near the area of release throughout the study) was detected. Over the three years of the study, the relocation efficiency was 80%.

The effective range of the telemetry equipment, defined as the maximum distance from the beacon tag at which its signal could still be detected, was 0.5 nautical miles (nmi) (0.96 km). To ensure over-coverage, a survey grid was established with 0.5-nmi intervals between monitoring stations in 1998 and 1999, reduced to 0.3 nmi (0.58 km) in 2000 to account for an observed decay of transmitter power.

The surveys of Placentia Bay (Fig. 1), which included all known spawning grounds, took approximately two weeks. Deep areas in which cod were rarely located during 1998– 2000 (Lawson and Rose 2000; G.A. Rose, unpublished data) were not surveyed. In 2000, vessel constraints dictated that only the head of the bay could be surveyed (Fig. 1*c*), but in prior years no tagged fish were relocated in other areas. Surveys of the Bar Haven spawning ground were repeated (the timing and number depending on the weather and ship availability) over the 2- to 3-month spawning season, and in all years were terminated when no tagged cod were located for several days.

Additional telemetry

Periodically during the survey years, acoustic surveys were conducted both within and outside of Placentia Bay. All located aggregations of cod were checked for the presence of tagged fish. None were relocated during these checks, except in December 1999 when four individuals were relocated within the bay, including two that were not otherwise accounted for in the spawning-season surveys or by the fishery.

Transmitter returns

A commercial fishery was operative during each year of this study. A reward of $100 was offered for the return of transmitters with information on date and location of capture. All fish caught were reported to have been in good condition, indicating adequate recovery from the surgery. All but one of 15 tags returned were still transmitting.

Homing rate calculation

Homing was calculated as the proportion of tagged fish that returned to Bar Haven during the spawning season:

$$\frac{(\text{observed})e^{-1}(1-f)^{-1}}{(\text{tagged})(1-M-F-Z_{\text{tag}})}$$

In the numerator, the number of tagged individuals observed ("observed") at Bar Haven each spawning season was adjusted to account for a relocation efficiency (e) of 80% and a transmitter failure rate (f) of 6%. The denominator (i.e., the number of tagged fish at liberty during each survey) was calculated as the number of fish tagged ("tagged"), less natural mortality (M was set to 0.2), tagging-induced mortality (Z_{tag} = 6%, based on conventional tagging data for Placentia Bay during the same years as this study; N. Cadigan, Department of Fisheries and Oceans, St. John's, Nfld., personal communication), and fishing mortality (F). The fishing mortality was calculated as the proportion of tagged fish for which transmitters were returned ("returned"), adjusted for a tag-underreporting rate (u) of 35% (based on conventional tagging data; N. Cadigan, personal communication):

$$F=\frac{(\text{returned})(1+u)}{48}$$

Randomization tests

Given the larger sampling effort at Bar Haven relative to other parts of the bay, it was necessary to evaluate whether the proportion of tagged fish that was relocated at Bar Haven was a result of chance. Our dataset consisted of one record for every time our hydrophone went into the water, including observations on the location, time, and number of fish (if any) relocated. We performed 1000 tests in which the fish-relocation column was randomly redistributed relative to the date and location columns. As such, there was a greater chance that fish would be "relocated" in areas where sampling effort was concentrated. For each of the 1000 different random configurations, we recorded the number of fish "located" at Bar Haven. Given the distribution of those values, it was possible to calculate the probability that the observed value occurred by chance if tagged cod were randomly distributed.

Results and discussion

Our data indicate that Bar Haven cod showed a marked degree of homing. All fish relocated in subsequent spawning seasons were within 10 km of the Bar Haven spawning grounds, where the fish were originally tagged (Figs. 1*a*–1*c*). The majority were relocated within a few hundred metres of the tagging site. The fate of the nonrelocated fish remains uncertain. However, none were observed during the spawning season at other known spawning grounds in Placentia Bay. The probability of relocating no fish at the other known spawning grounds, given our sampling effort, is <0.02 (compared with a null distribution generated under the hypothesis of a random distribution of tagged fish among the spawning grounds). Moreover, no tagged fish were relocated in any cod aggregation located during spawning season acoustic surveys throughout the bay except at Bar Haven. Under a null hypothesis that tagged fish were randomly distributed throughout the bay, the probability of not relocating any outside the Bar Haven area during the spawning period with the design employed was <0.00003. Given the slim probability that our results were a function of sampling effort, we conclude that during spawning a much greater proportion of tagged fish were at Bar Haven relative to other locations in the bay. It is important to note, however, that at other times of year (i.e., non-spawning season), tagged cod were relocated using telemetry and caught in the fishery at many other sites both within and outside the bay.

Table 1. Homing rates for Bar Haven (BH) cod in 1999 and 2000, and the parameters used in their calculation.

A	B	C	D	E [D/48]	F	G	H	I	J [48(1–E–F–G)–HD]	K [J–IJ]	L [(B/K)/C]
1999	8	0.8	6	0.13	0.2	0.06	0.35	0.0667	27	26	0.39
2000	6	0.8	15	0.31	0.2	0.06	0.35	0.0667	15	14	0.53
Both years	3	0.8	15	0.31	0.2	0.06	0.35	0.0667	15	14	0.26

Note: A, year; B, number of cod relocated at BH during spawning season; C, efficiency of telemetry gear; D, cumulative number of transmitters returned from the fishery; E, fishing mortality; F, natural mortality; G, tagging-induced mortality; H, rate of tag under-reporting in fishery; I, rate of transmitter failure; J, number of cod alive at spawning time; K, number alive with functioning tags; L, homing.

Fifteen transmitters were returned through the fishery until June 2000. Fishery recaptures (Fig. 1*d*) occurred in every month except during the peak spawning season (March to May) when the fishery was restricted. All but two recaptures were made in Placentia Bay along known migration pathways to and from Bar Haven (Lawson and Rose 2000): one in September 1998 in Conception Bay on the northeast coast and another in February 2000 about 180 km off of the south coast of Newfoundland. Both out-of-bay recaptures were consistent with known migration patterns (Lawson and Rose 2000). Including fishery returns and all telemetry surveys (three spawning years, and haphazard sampling in December 1999), a full 67% of tagged fish were accounted for over the course of the study.

It is important to note that Bar Haven cod are known to migrate out of the spawning area during summer. Conventional tagging data (e.g., Lawson and Rose 2000) indicate that Bar Haven cod move to the outer part of the Bay (90–110 km) and sometimes as far as Trinity Bay (500 km) during summer. During this study, relocations at Bar Haven declined to zero by early summer in all three years. Moreover, very little fishing effort occurred outside the bay, yet two transmitters were recovered a long way from Bar Haven (one in Conception Bay and one on St. Pierre Bank).

What proportion of tagged fish successfully homed? During the two surveyed spawning seasons subsequent to tagging (1999 and 2000), eight and six tagged fish were relocated, respectively. Three fish were relocated at Bar Haven in all three years. Homing rates corrected for mortality, under-reporting, and tag failure for the 1999 and 2000 spawning seasons were 39% and 53%, respectively (Table 1). Multiyear homing was observed in 26% of cod tagged (Table 1). Although these estimates are somewhat sensitive to the rates of tagging-induced mortality and fishery under-reporting, when either parameter was set at 0 homing was never less than 39% in 2000. In reality, the values of these parameters were likely underestimates, given that they were derived from externally attached tagging studies, and we consider the homing estimates presented in Table 1 to be conservative. In at least one known case, a transmitter (of unknown identity) was thrown overboard because the fisher did not want to possess such a tracking device. Moreover, homing percentages are limited somewhat by survey effort, especially in 1999, when spawning occurred early and surveys missed a portion of the spawning.

We have demonstrated for the first time that individual cod are capable of precise homing to a spawning ground over multiple years. In addition, because Bar Haven cod are well known to perform long-distance migrations (several hundred kilometres) and to leave the bay between spawning periods (Lawson and Rose 2000), it is likely that homing was achieved over long distances. In a similar but smaller-scale study, Green and Wroblewski (2000) reported that in Gilbert Bay, a small inlet (only a few square kilometres in area) on the southern Labrador coast, tagged cod tended to stay in or return to specific locations in the bay, where they over-wintered and spawned. No cod showed any tendency to leave the bay, despite unimpeded access to the open ocean. Small-scale homing was observed in one year, but the battery life of the transmitters used by Green and Wroblewski (2000) was only 10 months, hence no individual could be tracked over multiple spawning seasons. Large-scale conventional tagging studies have led to inferred homing rates of between 71% and 92% for Northeast Arctic cod tagged at Møre and Lofoten, Norway (Godø 1984) and between 72% and 79% for cod tagged at the spawning grounds off of southwest Iceland (Jónsson 1996). However, the scale of these studies was very large, and fish were considered to have homed if they returned to any part of an extensive region of coastline (tens to hundreds of kilometres). The scale over which we measured homing was much smaller (a few kilometres), and included only one spawning site in a large bay within and beyond which cod migrate annually.

For marine fishes, assumptions of broad stock structure and little evidence of homing have laid the foundation for management being conducted over very large oceanic regions (hundreds of thousands of square kilometres) encompassing multiple spawning grounds. For example, Newfoundland cod fisheries are managed over spatial scales greatly exceeding those of the stock structure suggested by our results and by recent genetic studies (e.g., Ruzzante et al. 2000). Such management could inadvertently cause differential substructure overfishing, local extinctions, and reductions in productivity (Frank and Brickman 2000).

Although straying to neighbouring spawning grounds was not observed in this study, the number of unaccounted-for fish implies that straying did occur, perhaps to areas outside Placentia Bay. The straying rates inferred from our results suggest potential genetic exchange among adjacent populations. We believe that cod have achieved a life-history balance between homing and straying that maintains population stability on the one hand, yet on the other does not preclude recolonization. This balance is likely to affect the rate of recolonization and recovery of depleted elements of putative cod metapopulations (Smedbol and Wroblewski 2002). Moreover, the relatively strong homing evidenced in our study implies a moderate rate of range expansion and recolonization, even when spawning populations are relatively large, as they have been at Bar Haven. Several predictions have been made that Newfoundland cod would rebuild at rates calculated from historical data (e.g., Myers et al. 1997), but these rates have not been achieved (Hutchings 2000).

Based on the present findings, we conclude that homing behaviour in Atlantic cod impedes quick recolonization of depopulated spawning grounds and has led to a governed rate of recovery.

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A new ageing method for eggs of fish species with daily spawning synchronicity

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Abstract: A new method for ageing staged eggs of fish is presented. The method is intended for species that show spawning synchronicity and for which the egg phase can be classified into development stages, each of which lasts less than a day, such as sardines and anchovies. It combines biological information on the daily frequency of spawning and egg development rates, via a probabilistic resampling method. A general methodology that allows the use of models of daily spawning frequency and egg development as a function of temperature is provided and applied to sardine egg data from three surveys in northern Spain. Unlike previous ageing methods, the proposed method allows for the variability of egg ages in a way that reflects the extent of the assumed daily spawning period, and estimates of the uncertainty in the stage-to-age conversion can be obtained. These estimates of uncertainty can be incorporated into subsequent analyses that involve age as a covariate, such as in the daily egg production method (DEPM), thus allowing more reliable estimates of the variance of egg production.

Résumé : On trouvera ici une nouvelle méthode pour la détermination de l'âge chez des œufs de poissons qui se développent par stades. La méthode est destinée à s'appliquer aux espèces, comme les sardines et les anchoies, chez lesquelles la fraye est synchrone et la période embryonnaire peut être divisée en stades de développement, chacun d'une durée de moins d'une journée. Elle combine les données biologiques sur la fréquence journalière de la fraye et sur les taux de développement des œufs à l'aide d'une méthode de re-échantillonage probabiliste. Nous présentons une méthodologie générale qui permet d'utiliser les modèles de fréquence journalière de fraye et de développement embryonnaire en fonction de la température et nous l'appliquons à des données sur les œufs de sardines provenant de trois inventaires du nord de l'Espagne. Contrairement aux méthodes antérieures de détermination de l'âge, la méthode que nous proposons tient compte de la variabilité des âges des œufs de façon à refléter la durée assumée de la période de fraye journalière; elle fournit aussi des estimés de l'incertitude reliée à la conversion des stades en âges. Ces estimés d'incertitude peuvent ensuite être incorporés dans des analyses subséquentes qui utilisent l'âge comme co-variable, telles que la « méthode de production journalière d'œufs », et ils permettent d'obtenir des estimés plus fiables de la variance de la production d'œufs.

[Traduit par la Rédaction]

Introduction

Egg production methods, mainly the annual egg production method (AEPM) and the daily egg production method (DEPM), are widely used in fish stock assessment (Gunderson 1993). Both methods involve estimating the production of eggs (total annual production in AEPM and a daily rate in DEPM), and back-calculating the adult stock that spawned the eggs by using adult parameters such as fecundity (annual fecundity in AEPM or batch fecundity in DEPM; Hunter and Lo 1993) and sex ratio of the stock.

Several approaches have been used to estimate the total number of eggs in the spawning region over the period of interest. For species with eggs that develop slowly, only eggs in the first stage of development are used in the analysis (for rationale, see Anonymous 1991; Priede and Watson 1993). For species with fast-developing eggs, information from all stages is used to increase the precision, because the proportion of sampled eggs in the first stage is low. For pelagic eggs, mortality over all stages is substantial, and when all stages are to be used, both the egg production and the mortality rate are usually estimated by fitting a mortality curve to the abundance of sampled eggs classified in age classes (Gunderson 1993). In these cases, the daily egg production rate is generally estimated as the intercept of the mortality curve (i.e., the number of eggs of age 0 produced per day and per square meter), and the standard error of the daily egg production rate is estimated either using standard analytic formulas or using computer intensive methods (e.g., bootstrap, Lo et al. 1996; or jacknife, Motos 1997). Thus, assigning ages to the sampled eggs is a necessary step to estimate egg production rates in the cases where a mortality curve is fitted to the data.

To assign ages to the sampled eggs, these are first classi-

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fied into development stages with the aid of morphological keys (e.g., Ahlstrom 1943; Gamulin and Hure 1955 for sardine; Moser and Ahlstrom 1985 for anchovy). Additional information about the duration of the stages as a function of sea temperature and the distribution of ages within each stage is required to allow the stage-to-age conversion. This information is usually acquired from temperature-controlled experiments (Lo 1985; Miranda et al. 1990), in which the age range for eggs in different stages and at different temperatures is measured, and models that relate mean age for any stage and temperature are fitted to the data (Lo 1985).

When spawning is concentrated in a fraction of the day, assigning ages to stages is simplified. Knowledge of the daily spawning frequency of a given species can be acquired from ovary studies of adult fish (Hunter and Macewicz 1985; Picquelle and Stauffer 1985; Zwolinski et al. 2001). Using information from ovary studies and a temperature-dependent model of egg development, Lo (1985) designed an automatic ageing procedure for the assessment of the Pacific Northern Anchovy (*Engraulis mordax*) stocks. Nevertheless, only a fixed peak time of spawning and the limits of the daily spawning period, inferred from the ovary studies, are used as the daily spawning synchronicity information in the work of Lo (1985), while the shape of the underlying frequency distribution of spawning events is neglected. Also, as the time of spawning is treated as a fixed parameter, no errors associated with the ageing procedure can be estimated using that method. Thus, when daily egg production rates are estimated, the uncertainty related to the mean age of each age class (normally daily cohorts) of eggs is ignored.

Here a new ageing method is proposed. It allows the inclusion of prior knowledge about the daily spawning frequency in the ageing procedure, via a probability density function (PDF) of spawning time. It also allows the error associated with the distribution of ages to be estimated, and thus to be included in subsequent procedures that involve estimates of egg ages. The method can be applied to species that show daily spawning synchronicity and for which the egg phase can be classified in development stages that last less than a day. To apply the method, it is necessary to obtain models that relate mean age for all stages of the target species to a range of temperatures and to have a suitable model of the spawning times PDF. Suitable stocks include various species of sardine and anchovy, some stocks of which have great importance for local economies, and most of which are currently assessed by DEPM (see examples in Gunderson 1993).

In this paper, first the new ageing procedure is described in detail as a general method that can be applied to stocks of synchronous spawning fish for which both a stage-to-age model of any given specific formula and a PDF of spawning times are available. Also, a graphical method that allows visual validation of the assumptions made, as well as comparison of the results obtained from this method and those obtained with the previous ageing method proposed by Lo (1985), is described. Then, the formulation of the ageing procedure is adapted to use the available information in a specific example regarding sardine (*Sardina pilchardus*, Walbaum) stocks off the north coast of Spain (García et al. 1991, 1992; Lago de Lanzós et al. 1998). A brief description on how to use the new estimates of age in the DEPM context is also presented and the results of the application of the method in the sardine example are described and compared with results from previous ageing methods. The benefits of using the new procedure in the DEPM context are shown, and the general benefits and problems of the new method are treated in the discussion.

Materials and methods

General ageing procedure

The ageing procedure presented here has two components: (*i*) a stochastic model relating stages and ages for given temperatures (the "stage-to-age model"), and (*ii*) a probability density function (PDF) of spawning times. All notations used in the paper, including the general formulation of models (*i*) and (*ii*), are shown in Appendix 1.

Stochastic model

The stochastic model used in this paper is a modified version of the available deterministic stage-to-age model, fitted to data from temperature-dependent experiments on egg development. This model usually follows the general formula of Lo (1985):

$$(1)\qquad \bar{a}_{i,t} = \theta_1 e^{(\theta_2 t + \theta_3 i)} i^{\theta_4}$$

where $\bar{a}_{i,t}$ is the mean age of stage i at incubation temperature t, and θ is the vector of parameters (θ_1, θ_2, θ_3, and θ_4) whose estimates can be obtained by different fitting procedures, for example, using a log transformation of the mean age for each stage at each temperature and fitting the model by least squares (Lo 1985).

The stochastic version of the model described by eq. 1 incorporates two sources of variability. (*i*) To predict individual egg ages given stage, as opposed as mere mean ages for stage, a distribution of ages for each stage is assumed. There are different choices for the age distribution within a stage. If mortality within a stage is neglected and the age range for any given stage and temperature is known, a uniform distribution of ages within the age range for each combination of stage and temperature can be assumed. On the other hand, if mortality is considered, there should be fewer older eggs within each stage. (*ii*) Also, an error distribution for the residuals about the stage-to-age model is assumed. With a least-squares-fitting method, it is natural to assume that residuals are normally distributed, but if a more complex fitting procedure (e.g., Generalized Linear Models, GLM; McCullagh and Nelder 1989) is used, other error distributions might also be reasonable.

When data from rearing experiments are available, an adequate stochastic stage-to-age model can be obtained from the data. For example, a stage-to-age curve can be fitted directly to data for individual egg age and stage, given that ages within each stage follow a common distribution through all stages (e.g., one that accounts for increasing variance in older stages). Otherwise, a more theoretical model can be constructed (see the section on application below). In this section, we will assume that we have an adequate stage-to-age stochastic model, of a general form $g(a : i, t, \theta, \varphi_{i,t})$, where θ are the parameters of the initial deterministic stage-to-age model and $\varphi_{i,t}$ are the parameters related to the distribution of ages within a given stage and for a given temperature. For simplification, we will use $g(i, t)$ as $g(a : i, t, \theta, \varphi_{i,t})$. In the example below, we will explicitly create a stage-to-age stochastic model based on the available information and assumptions and use it to test the ageing procedure.

PDF

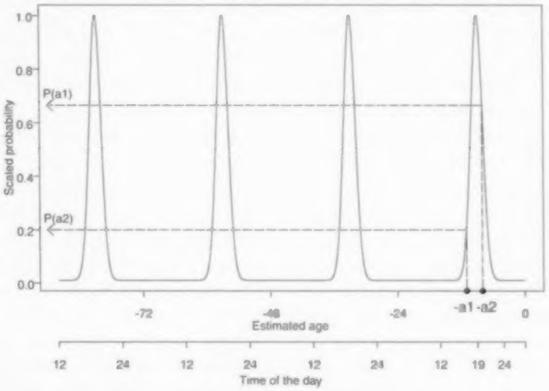
Information about the PDF of spawning time can be obtained from different sources. One of the most common is through ovary studies (Hunter and Macewicz 1985; Picquelle and Stauffer 1985), although other sources of information, like distribution of stage I eggs (Motos 1994) can also be used to construct the PDF of the spawning times. Assuming that the studied species shows daily spawning synchronicity, with a fixed daily distribution of spawning times and a constant daily egg production rate through the survey period, the PDF of spawning times would be represented by a curve with daily cyclic peaks of spawning events. The PDF of spawning times can be approximated using frequency histograms of daily spawning events, obtained from experimental ovary studies in which the times when fish are ready to spawn or have just spawned are observed. When experimental data are accurate enough, more sophisticated techniques like kernel density estimates can be used to obtain a continuous PDF. On the other hand, when the available information about spawning time is not very accurate, a prior distribution of the spawning time can be postulated using some previous knowledge from experts (Smith and Hewitt 1985). Again, for the general ageing procedure we will assume that we have an adequate spawning times PDF, of a general form $f(\tau;\beta)$, where τ is time of day and β is the set of parameters needed to construct the model. For simplification, we will use $f(\tau)$ to represent $f(\tau;\beta)$. As in the case of the stage-to-age model, we will derive a specific spawning time PDF model in the example below.

Once a PDF for spawning times and a stochastic stage-to-age model have been obtained, the procedure to assign ages to each sampled egg is based on sampling from the initial vector of ages (predicted by the stochastic stage-to-age model), with sampling probabilities obtained by evaluation of the spawning times PDF at the time when each egg has been spawned. Explicitly, the procedure works as follows (see Fig. 1). The spawning times PDF must be located in relation to the survey time; therefore, the survey time (i.e., the time at which a given sample was taken) is located at the origin of the time scale. The PDF of spawning times is then located with reference to the survey time, so a number of daily spawning cycles occur before the survey time. For example, if the spawning peak is at 19:00 and a given survey time was at 02:00 the next day, then the first "peak" of the spawning times PDF will be at time $-[2 + (24 - 19)] = -7$, the next one at time $-7 - 24 = -31$, and so on. The eggs last in the sea only a few days before hatching; this period determines the number of spawning peaks required. Once the PDF is located in reference to the survey time, sampling from random ages predicted by the stochastic model is carried out as follows. First, an initial age $a_{\mathrm{initial},j}$ for each egg j ($j = 1,\ldots,N_{\mathrm{eggs}}$) in stage i ($i = 1,\ldots,N_{\mathrm{stages}}$) and sampled at temperature t, is generated as a random variable from $g(i, t)$. Then, the probability that an egg was spawned at time $\tau = -a_{\mathrm{initial},j}$ (so an egg j has an age a_{initial} at the time of the survey) is evaluated using the PDF of the spawning time, i.e., $p(\text{egg spawned at } \tau = -a_{\mathrm{initial},j}) = f(\tau = -a_{\mathrm{initial}})$. This probability will be used to accept or reject a given random age produced by the stage-to-age model. In the case that the initial age for a given egg j, $a_{\mathrm{initial},j}$, is rejected, a new age for that egg will be produced by the stochastic stage-to-age model. The criterion to accept a given random age predicted by the stochastic stage-to-age model works as follows. A random number r_j from a uniform distribution between 0 and max $(f(\tau))$ is generated for each egg, and $a_{\mathrm{initial},j}$ is accepted if $r_j < f(-a_{\mathrm{initial},j})$. So if $r_j < f(-a_{\mathrm{initial},j})$, then $a_{\mathrm{final},j} = a_{\mathrm{initial},j}$. To simplify this rejection method, the PDF is rescaled by dividing it by max $(f(\tau))$:

$$f'(\tau) = \frac{f(\tau)}{\max(f(\tau))}$$

so it will vary between 0 and 1, and thus r_j is always generated as a random number between 0 and 1. Using this rejection method, any given age whose back-calculated spawning time has a probability of, for example, 0.7, obtained by evaluation of the PDF at that time of the day, will have a 70% probability of being accepted.

Fig. 1. A graphical (schematic) representation of the ageing procedure. The procedure is illustrated with two different ages generated from the stage-to-age model (a_1 and a_2). The spawning peaks (at 19:00 each day) are located in relation to the survey time (02:00), and the scaled probability of the generated ages ($p(a_1)$ and $p(a_2)$) is obtained by evaluating the scaled PDF of spawning times at time $-a_i$.



The decision on the maximum number of times that the sampling procedure (generation of $a_{\mathrm{initial},j}$, evaluation of $f(-a_{\mathrm{initial},j})$ acceptance or rejection of $a_{\mathrm{initial},j}$) may be iterated for a given egg until either an age is accepted or the procedure fails to obtain an acceptable age for that egg depends on the objective of the work and the assumed spawning times PDF. Suppose the probability of spawning is only positive for a restricted period of the day:

$$\begin{cases} f(\tau) > 0 & \tau \in [\tau_0, \tau_1] \\ f(\tau) = 0 & \tau \notin [\tau_0, \tau_1] \end{cases}$$

It is then possible that some of the eggs will never fall into the range of acceptable ages, because the back-calculated spawning time of those eggs is outside the limits of the anticipated range of spawning times within a day $[\tau_0, \tau_1]$. Thus, those eggs have an anomalous age according to our prior beliefs. This could be due to our prior beliefs being wrong, or to errors in the staging of these eggs. For example, Motos (1994) found eggs of stage I from anchovy, a species with markedly synchronous spawning, at nearly all times over the day. As the duration of those eggs is substantially less than a day, he concluded that these eggs were probably unfertilised eggs that were misclassified as stage I eggs. Also, other biological reasons such as unusual development rates can affect the accurate stage-to-age conversion of some eggs. In these cases it may be best to exclude these eggs from the analysis. Alternatively, and in particular if the PDF of the spawning time is not based on empirical evidence, one may want to allow eggs spawned at any time during the day to be accepted. In this case the PDF of spawning time can be modified to include a small probability of spawning occurring at times during the day outside the peak spawning period.

The initial ages ($a_{\mathrm{initial},j}$; $j = 1,\ldots,N_{\mathrm{eggs}}$) used in the ageing procedure are random variables, and the time of spawning is not a fixed parameter, but another random variable. Thus, by repeating the ageing procedure, different sets of final ages are obtained and these can be used to estimate the error in the ageing procedure. These can also be used to model the uncertainty associated with ages in analyses that involve age as a covariate (see the example regarding the estimation of daily egg production rates below).

A graphical method to visualise differences between ageing methods

A simple graphical method was developed to visualise the differences between the results obtained from the method proposed here and the results obtained with a previous ageing method developed by Lo (1985). The method also allows checking for inconsistencies between the ages predicted by the stage-to-age model and the spawning times PDF. Egg ages are converted to ages at midnight before the sampling occurs (i.e., ages that those eggs would have if they were sampled at midnight). The resulting values are made negative to compare their distribution with the PDF of spawning times, so the plotted converted age $a_{\mathrm{initial},j}{}^{*}$ would be

$$a_{\mathrm{initial},j}{}^{*} = -(a_{\mathrm{initial},j} - \tau_s) = \tau_s - a_{\mathrm{initial},j} \tag{2}$$

where τ_s is the survey time and $a_{\mathrm{initial},j}$ is the predicted age from the stochastic stage-to-age model. The converted age $a_{\mathrm{initial},j}{}^{*}$ can now be regarded as a spawning time in a linear scale (instead of a cyclic 24-h scale). Thus, a frequency distribution plot of the converted ages can be compared directly with the spawning times PDF, given that the PDF is also located in relation to midnight hour. The same procedure can be used to convert the accepted ages $a_{\mathrm{final},j}$ into standardized ages $a_{\mathrm{final},j}{}^{*}$ and to standardize the ages produced from the traditional method ($a_{\mathrm{trad},j}{}^{*}$). These changes allow direct graphical comparison of the distribution of spawning hours predicted by the spawning time PDF with back-calculated spawning hours obtained from the stage-to-age model, from the whole ageing procedure and with other ageing procedures (e.g., from Lo 1985).

An application of the method: ageing sardine eggs

In this section we apply the method to data from sardine DEPM surveys off the Spanish north coast in 1988, 1990, and 1997. These surveys are described in García et al. (1991, 1992) and Lago de Lanzós et al. (1998). They involve simultaneous egg and adult sampling, to allow all parameters of the DEPM to be estimated. The results are compared with results from the ageing procedure of Lo (1985) (the traditional ageing procedure), which has been the standard procedure for DEPM assessment of sardine spawning biomass off Spain until 2000.

The traditional ageing procedure is applied to the data using a modification of the Fortran program Stageage, developed by Lo (1985) and adapted for use with the Spanish sardine stocks by García et al. (1991). The deterministic stage-to-age model fitted to data from growth experiments has the general form of eq. 1, and the parameter estimates are those found by Pérez et al. (1992) and Miranda et al. (1990) (see also Fig. 2):

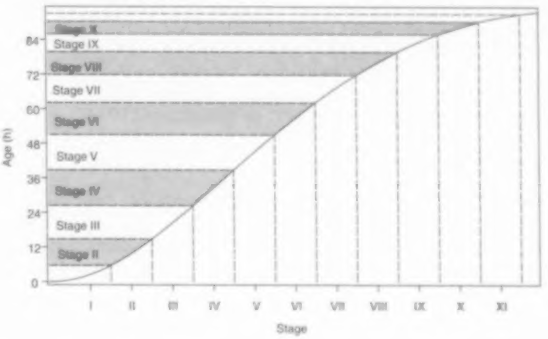
$$\bar{a}_{i,t} = 17.72\,\mathrm{e}^{-(0.136t+0.173i)}\ i^{2.222} \tag{3}$$

For Spanish North-Atlantic sardine, the estimated spawning peak hour, obtained by analysis of ovary data, is 19:00 GMT (Greenwich Mean Time) and the spawning range is between 14:00 GMT and 21:00 GMT (Pérez et al. 1989; Olmedo et al. 1990).

To apply the new ageing procedure, and following the ideas of Smith and Hewitt (1985), the PDF of spawning time is assumed to be a series of normal distributions with mean equal to the estimated spawning peak (19:00 GMT) and variance of 2.25. This gives a distribution with 2.5 and 97.5 percentiles corresponding to 16:00 and 22:00 GMT, respectively, similar to the spawning period estimated by Pérez et al. (1989). As this PDF is not directly based on empirical data, a minimum probability baseline of 0.01 is added to allow for ageing of eggs that appear to have been spawned outside the anticipated spawning period. Sardine eggs in the Cantabric Sea hatch within three or four days (Pérez et al. 1989), so only four spawning peaks are used to analyse the data from each of the samples.

To convert the model described in eq. 3 into a stochastic model, two types of errors are assumed. (*i*) A uniform distribution of ages within each stage was assumed to account for the possible age range of individual eggs at any stage. Although this assumption neglects natural mortality within stages in the ageing method, it has been used as an underlying assumption in the traditional ageing method. Thus, for comparative purposes, it is also adopted in this example. (*ii*) Also, a log-normal error distribution of the mean age for each stage is assumed to account for the residuals of the stage-to-age model.

Fig. 2. Age range for sardine eggs at each stage of development at 13°C (Miranda et al. 1990).



The uniform distribution of ages within each stage is constructed as follows. First, the age range for each stage *i* at a given temperature *T* is assumed as the interval between the mean age predicted by model (eq. 3) for a stage value of $(i - 0.5)$ and that of $(i + 0.5)$, except for the first stage, where the lower age limit is assumed to be zero (see Fig. 2). Then, uniform samples of ages from a given stage are obtained as samples from a uniform distribution within the age limits of that stage.

As an example, we will illustrate how to generate an age for an egg in stage III at a given temperature *T*. First, the lower and upper age limits of that stage for that temperature are found by fixing $t = T$ and substituting $i = 2.5$ and $i = 3.5$, respectively, in eq. 3. Then, a random age r_{age} is obtained as a sample from the uniform distribution defined by the lower and upper age for stage III at temperature *T*. Once r_{age} is predicted, the logarithm of a_{initial} is generated as a random value from a normal distribution with mean equal to the logarithm of r_{age} and variance estimated from the residuals of the deterministic stage-to-age model (eq. 3):

$$\log(a_{\mathrm{initial}}) \sim N(\log(r_{\mathrm{age}}), \hat{\sigma}^2)$$

where $\hat{\sigma}^2$ represents the estimated variance of the mean age values around the deterministic stage-to-age fitted model, on a log scale. An estimate of σ^2 was not available for the present work, but it is known that the variance explained by the model is a very high percentage of the total variance of the data (Pérez et al. 1992). Hence, a small variance of 0.012 was assumed.

Once the initial age of this egg is obtained (a_{initial}), and the scaled version of the PDF of spawning times $f'(\tau)$ is located with reference to the survey time, the PDF is evaluated at time $-a_{\mathrm{initial}}$ and a random number r_{cut} between 0 and 1 is generated, to apply the rejection method. If r_{cut} is smaller than $p(-a_{\mathrm{initial}})$ then a_{initial} is accepted, otherwise a new age is generated following the steps above and the rejection procedure is repeated until a given age is accepted. (In this case, we allow a small probability that an egg is spawned at any time outside the main spawning period, so that an age can always be found.)

Using the ages from the new method in the egg production rate estimate

The aged eggs in each positive station (i.e., stations located inside the limits of the spawning area, see García et al. 1992 for a detailed explanation) are classified in daily cohorts (i.e., eggs that were spawned the same day). The abundance of eggs in each daily cohort is converted into density, using the effective surveyed area

(Gunderson 1993), and a mortality curve is fitted to the density of eggs in each daily cohort and in each station. A total number of three cohorts was used in the analysis. Although sardine eggs can take as long as four days to hatch at the temperatures found in the sampled region, some eggs will hatch on the third day, and thus the fourth cohort was excluded from the analysis to avoid bias (Lo 1985). The mortality curve follows the general exponential mortality model described in Lo (1985) or Gunderson (1993):

$$D_{\mathrm{age}} = D_0\, e^{-z\mathrm{Age}}$$

where D_{age} is the density of eggs with mean age "age", z is the mortality rate, and Age is the mean age of the daily cohort. D_0 is the density of eggs of age 0, i.e., the daily egg production rate. The fitting procedure is based on a GLM (McCullagh and Nelder 1989) context, instead of the traditional least squares procedure, following the model below:

$$(4) \qquad E[D_{\mathrm{age}}] = g^{-1}(\log(D_0) - z\mathrm{Age})$$

where $E[D_{\mathrm{age}}]$ is the expected value of the density of eggs of age "age" and g^{-1} is the inverse of the link function (see McCullagh and Nelder 1989 for details). In this case the link function used is natural logarithm, and a negative binomial distribution family, which accounts for increasing variance as the density of eggs increases, was used in the fitting procedure. The negative binomial distribution has an extra parameter θ, which is iteratively estimated in the fitting procedure, using the procedure of Venables and Ripley (1997). Both parameters $\log(D_0)$ and $-z$ are estimated as the intercept and slope of the GLM model. The daily egg production rate is estimated as the exponential of the intercept of the model (i.e., D_0). Also, as more samples were taken in the area where a higher density of eggs was expected, weights that account for the uneven sampling were used in the fitting procedure (see García et al. 1991 for details). The coefficient of variation (CV) of the daily egg production rate is estimated by a modified parametric bootstrap procedure, in which not only the egg abundance is resampled from the distribution assumed in the model, but also the mean age of each cohort is resampled using the ageing procedure.

In the procedure, a vector of ages for all sampled eggs is estimated from the new ageing procedure. The eggs are then classified in daily cohorts, with a total number of three cohorts in each station. The mean age for each cohort is estimated as the average age of the eggs included in that cohort. If no eggs are included in a given cohort for a given station, then the mean age is estimated as the elapsed time between a random spawning time, produced from the spawning times PDF, and the sampling time of that station. The model described in eq. 4 is fitted to the data on egg density and mean age for each cohort in each station. A total number of 400 pseudosamples of egg density are obtained from the fitted density values, using a negative binomial distribution with parameters as fitted in the model (i.e., mean equal to fitted value and θ as estimated by the fitting procedure). Also, a total number of 400 pseudosamples, each one consisting of a vector of ages for all sampled eggs, are generated from the new ageing procedure. Each pseudosample is classified in daily cohorts, and a mean age for each cohort in each station for each pseudosample is estimated. The fitted model is then refitted to each pseudosample of egg density using a new pseudosample of mean cohort age. The point estimate of D_0 is obtained in each of the iterations and the variance of D_0 is the variance of the obtained vector of D_0 estimates. A corrected point estimate of daily egg production rate is also obtained from the bootstrap mean of the estimates of daily egg production (see Efron and Tibshirani 1993 for a detailed explanation on the bootstrap).

To compare the egg production estimate and its CV with those obtained with the traditional ageing method the egg production estimate using the traditional ageing method is estimated and its CV is also estimated using a parametric bootstrap, but in this case without iteratively using pseudosamples of age, because the traditional ageing method will always yield the same age. For comparative purposes, the point estimate and the CV of egg production obtained using both the traditional and the new ageing method are computed using standard analytic formulas, without including the error incurred from the ageing procedure.

Results

Figures 3, 4, and 5 show the distribution of the back-calculated spawning times based on (*i*) the initial ages produced by the temperature-dependent stage-to-age model, (*ii*) the final ages produced by the new ageing method, and (*iii*) the ones produced by the traditional method over the 1988, 1990, and 1997 DEPM surveys, using the graphical method described above. Positive values on the *x*-axis correspond to eggs that had not yet been spawned by the midnight before sampling occurred, so when their standardized spawning time is represented it becomes positive (see eq. 2).

It is important to note that the graphical procedure uses a different time origin from that of the ageing procedure. In the former, the PDF of spawning times is fixed in relation to midnight hour, and ages coming from different survey times are transformed to plot densities of estimated spawning times, whereas in the latter the survey time is fixed at the origin of the time scale and the PDF is located in relation to it.

The peaks of the PDF of spawning time are located at the same times as those where the maximum densities of the initial standardized ages predicted by the stage-to-age model occur, indicating good agreement between the two independent sources of information used in the analysis (i.e., the stage-to-age model and the assumptions about the spawning frequency) (Figs. 3, 4, and 5). However, there are some discrepancies in the case of small positive transformed age values (see the initial ages in Figs. 4 and 5). The ages of these eggs as predicted by the stage-to-age model are not accepted by the traditional ageing procedure, and instead those eggs are given a random age that corresponds to either the maximum or the minimum age for their stage at a given temperature (see Lo 1985). Nevertheless, as a small probability of spawning throughout the day was allowed, they are accepted in the new ageing procedure. Although the problem is similar to that found by Motos (1994), further investigation is needed before excluding these eggs from future analysis.

The back-calculated spawning times from the new ageing procedure ($a_{\mathrm{final}}{}^*$) have a similar distribution to the spawning times back-calculated using the stage-to-age model ($a_{\mathrm{initial}}{}^*$), as shown in the figures. Nevertheless, the dispersion of the spawning times around mean values for each day is smaller when applying the method, as the extreme values for each day have been excluded selectively using the rejection method described above. On the other hand, the traditional ageing procedure produces sharp histograms with large numbers of eggs with a common adjusted age. Note that the scales on the *y*-axis are different because of the aggregation of ages produced by the traditional method. Nevertheless, the total number of observations for each day is nearly the same for all days in all of the studied years (results not shown).

Figures 6, 7, and 8 show the distribution of the resulting ages within each stage, as well as the 95% age interval for

Fig. 3. Distribution of spawning times based on the 1988 daily egg production method (DEPM) survey. From top to bottom, (*a*) the PDF of spawning time, (*b*) the back-calculated spawning times obtained from the initial ages, and (*c*) the back-calculated spawning times obtained from the final ages of the new and the traditional ageing methods. Note the scales on the *y*-axis are different due to the difference in number of counts within a given interval for each method.

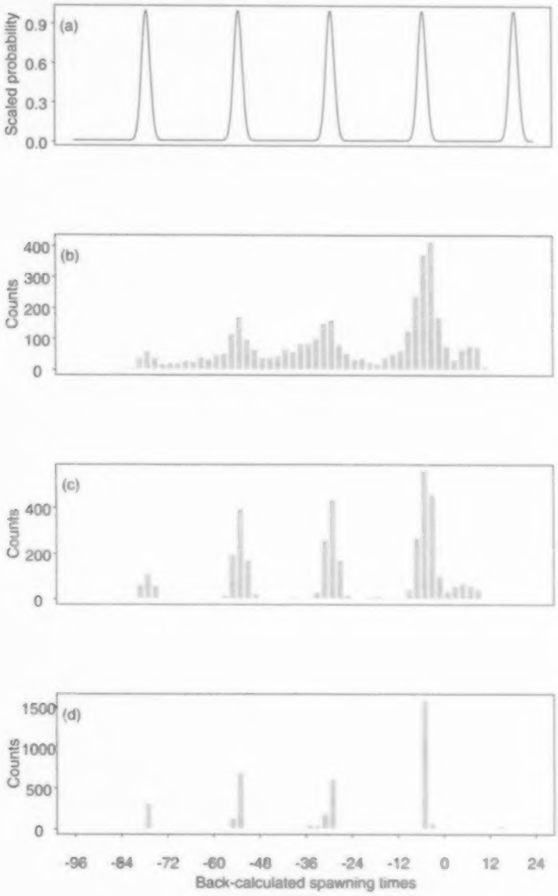
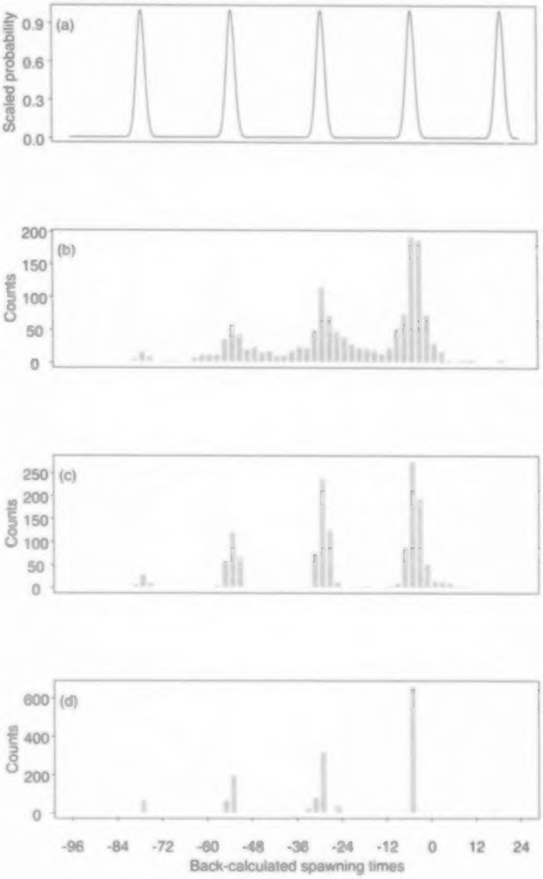


Fig. 4. Distribution of spawning times based on the 1990 daily egg production method (DEPM) survey. From top to bottom, (*a*) the PDF of spawning time, (*b*) the back-calculated spawning times obtained from the initial ages, and (*c*) the back-calculated spawning times obtained from the final ages of the new and the traditional ageing methods.



each stage from the stage-to-age model, for all years and for three different temperature intervals. The range of the resulting ages is within the 95% age interval predicted by the stage-to-age model, except two or three cases in which the age is very near the 95% limit, but outside it. Thus, the resulting ages are coherent with the ages predicted by the stage-to-age model. Nevertheless, in most of the cases the range of the obtained ages within each stage is narrower than the 95% limits of the ages predicted by the stage-to-age model. This indicates that the ageing procedure has selected only a certain interval of the whole range of possible ages for each stage and temperature.

Figure 9 shows the density of eggs together with their mean age within each day cohort for each sampled station, from both the traditional and the new ageing method, with the density axis in log scale to allow for better interpretation of the plots. Also, the fitted exponential mortality model is indicated in the figures. Both panels show a very similar pattern, as the ages obtained by the traditional and the new ageing methods are similar. Nevertheless, although the figure only shows a realization of the new ageing method, by iteration of the new method a new set of ages can be obtained, and thus the mean age for each cohort will be slightly modified in each iteration. The analytic estimates of the parameters (D_0 and z) of both mortality models (Table 1) are similar using both the traditional (D_0 = 82.87 eggs·m^{-2}·day^{-1}, CV = 19.6%; z = 0.01, CV = 40%) and the new ageing method (D_0 = 95.11 eggs·m^{-2}·day^{-1}, CV = 17.7%; z = 0.01, CV = 33.3%), and are comparable to the ones found in García et al. (1991). The small differences with the work of García et al. (1991) exist because in that work the egg production rate is calculated for different areas along the whole survey region, while here only a common egg production rate for all the positive strata of the survey area is estimated. The analytic estimate of the CV of the parameters of the

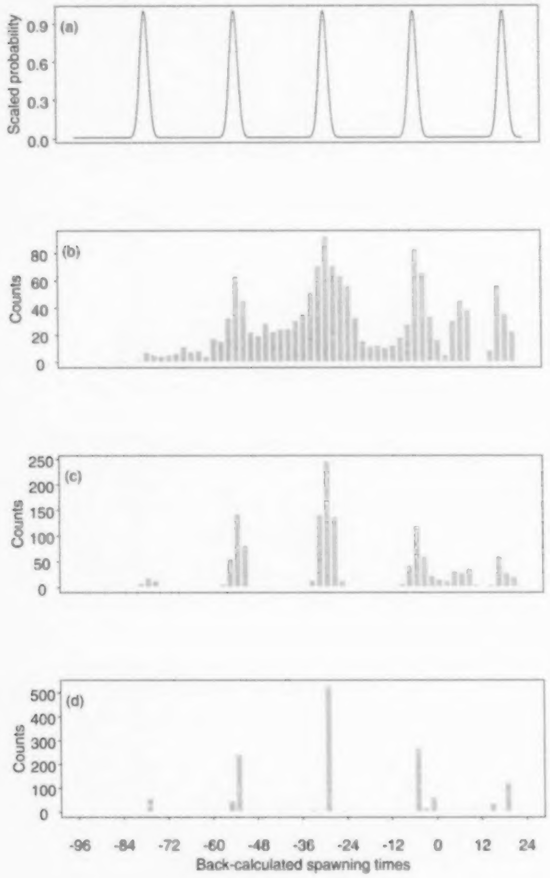


Fig. 5. Distribution of spawning times based on the 1997 daily egg production method (DEPM) survey. From top to bottom, (*a*) the PDF of spawning time, (*b*) the back-calculated spawning times obtained from the initial ages, and (*c*) the back-calculated spawning times obtained from the final ages of the new and the traditional ageing methods.

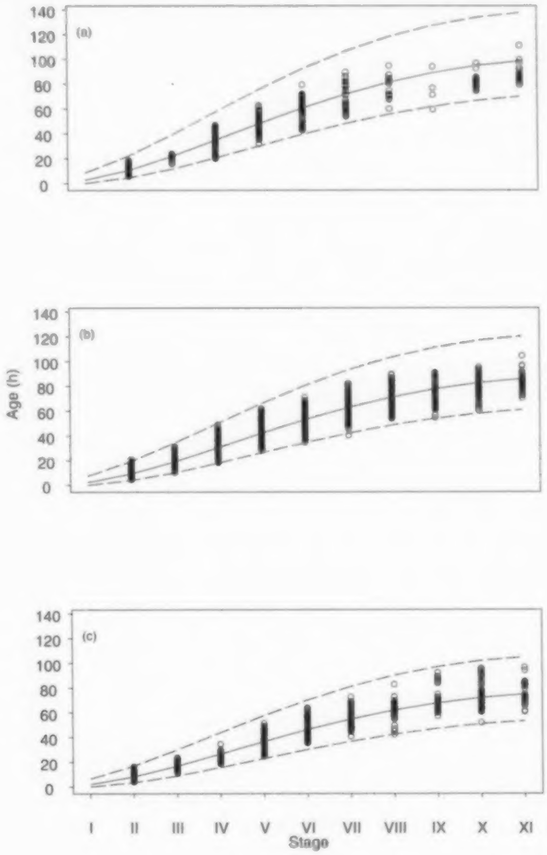


Fig. 6. Distribution of the resulting ages within stage for the 1988 sample. (*a*) Eggs found between 12°C and 13°C, (*b*) those found between 13°C and 14°C, and (*c*) those found between 14°C and 15°C. The solid line represents the mean age value for each stage as predicted from the stage-to-age model for the mean temperature of each range and the broken lines represent the range within 95% of the ages from the stage-to-age model lay.

mortality curve using the new ageing method (without the ageing error) are slightly lower than analytic estimates found when the traditional estimates of age are used, probably owing to the larger spread of ages in the older eggs, which distribute the abundance of older eggs throughout different cohorts. The corrected point estimate from the parametric bootstrap procedure (Table 1) is very similar to the one found using standard analytic procedures (D_0 = 81.86, CV = 19.3% using the traditional ages and D_0 = 92.20, CV = 19.2% using the new method ages, including the ageing error). Nevertheless, the CV of the egg production estimate using the new method ages is increased by about 8%, owing to the inclusion of the error in the ageing procedure.

Discussion

The new ageing method provides a way of assigning ages to eggs using information about daily spawning synchronicity and egg development. In comparison to previous ageing methods (Lo 1985), the method provides a framework in which the information or prior beliefs about any of the two basic elements of the method, the spawning times PDF and the stage-to-age model, can be incorporated in a flexible way, using models as complex as necessary to reflect current knowledge. Another major advantage of the new method is that the errors associated with the ageing procedure can be estimated, and if age is to be used in subsequent analysis, propagation of errors caused by the ageing procedure can be considered.

The simple graphical method described above allows direct comparison of the distribution of spawning times back-calculated from the stage-to-age model and the ones predicted by either the traditional or the new ageing method. The transformed ages used in this procedure are back-calculated spawning times, so they can also be compared with the spawning times PDF. This comparison allows for visual identification of inconsistencies between the two

Fig. 7. Distribution of the resulting ages within stage for the 1990 sample. Eggs found between (*a*) 13°C and 14.5°C, (*b*) 14.5°C and 16°C, and (*c*) 16°C and 17.5°C. The solid line represents the mean age value for each stage as predicted from the stage-to-age model for the mean temperature of each range and the broken lines represent the range within 95% of the ages from the stage-to-age model lay.

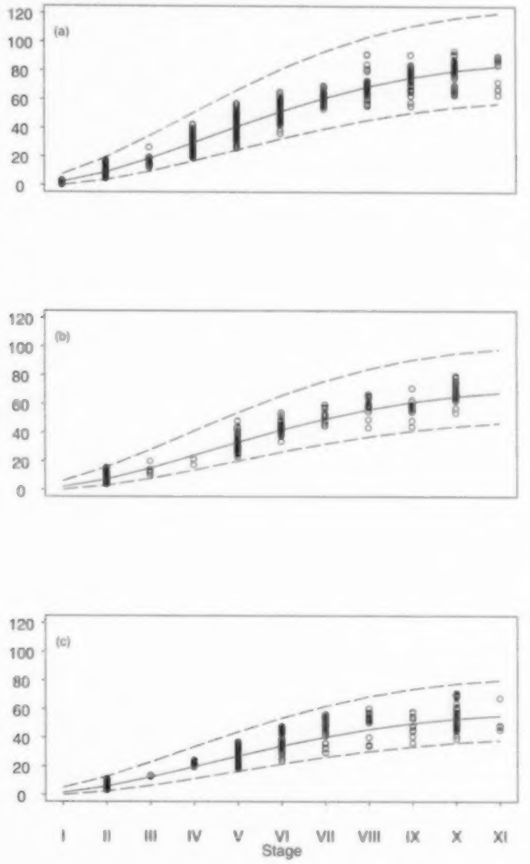
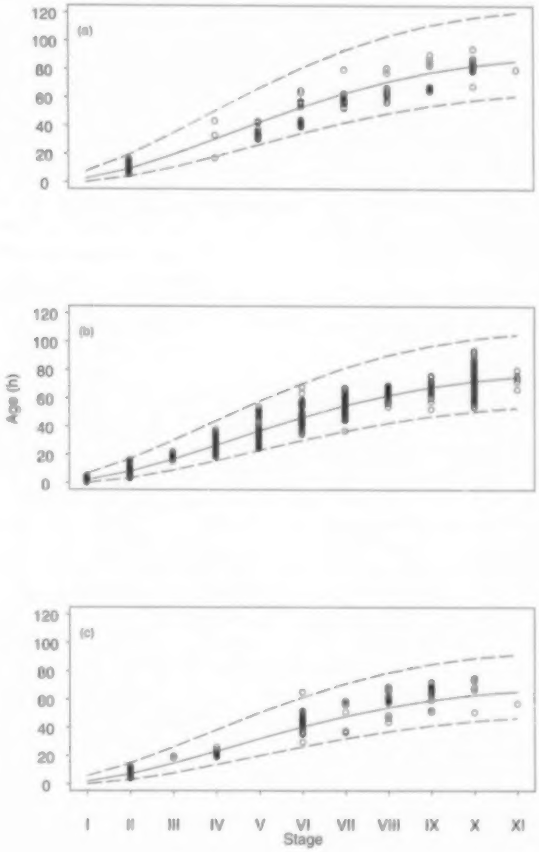


Fig. 8. Distribution of the resulting ages within stage for the 1997 sample. Eggs found between (*a*) 13°C and 14°C, (*b*) 14°C and 15°C, and (*c*) 15°C and 16°C. The solid line represents the mean age value for each stage as predicted from the stage-to-age model, for the mean temperature of each range, and the broken lines represent the range within 95% of the ages from the stage-to-age model lay.



models used in the ageing procedure, the spawning times PDF and the stage-to-age model. Also, the graphical method is an interesting tool to visually inspect the egg abundance trend over days. The abundance of each egg day-cohort (as defined in Lo 1985 and Gunderson 1993) is represented in the plots by the integral of the histogram within the age limits of each cohort. Each day-cohort is shown as a mode in the histogram of the standardized accepted ages, and thus the abundance trend along ages can be inspected by changes in the height and width of each mode. Estimates of mortality can in principle be obtained by fitting a mortality curve to this data, in a similar way as in the classical DEPM approach (Lo 1985; Gunderson 1993).

The results obtained in the example show that the new ageing procedure generates ages that are consistent with previous knowledge about the biology of the species. Both the back-calculated spawning times obtained using the stage-to-age model ($a_{\mathrm{initial}}*$) and the spawning times PDF show a similar pattern, with eggs being released only in the evening. Both the traditional and the new ageing procedure capture this feature and predict ages whose back-calculated spawning times are around 19:00, the assumed spawning peak.

The mean values of back-calculated spawning times for eggs spawned over the same day are similar using either the traditional ageing method or the new one. This can be seen in this study, where the transformed final ages from the two ageing methods ($a_{\mathrm{final}}*$, $a_{\mathrm{trad}}*$) show similar mean values. Nevertheless, the new ageing procedure produces ages that show dispersion in agreement with the extension of the daily spawning period. The dispersion of the back-calculated spawning times produced from the stage-to-age model have been filtered using the information from the spawning times PDF. Also, the resulting range of ages within stage is reduced in the ageing procedure in comparison with the initial range of ages for each stage predicted from the stochastic stage-to-age model. Nevertheless, the resulting ages are

Fig. 9. Log of the density of eggs classified in day-cohorts against mean cohort age, with ages from both *(a)* the traditional and *(b)* the new ageing methods. The solid line represents the mortality curve fitted to each dataset.

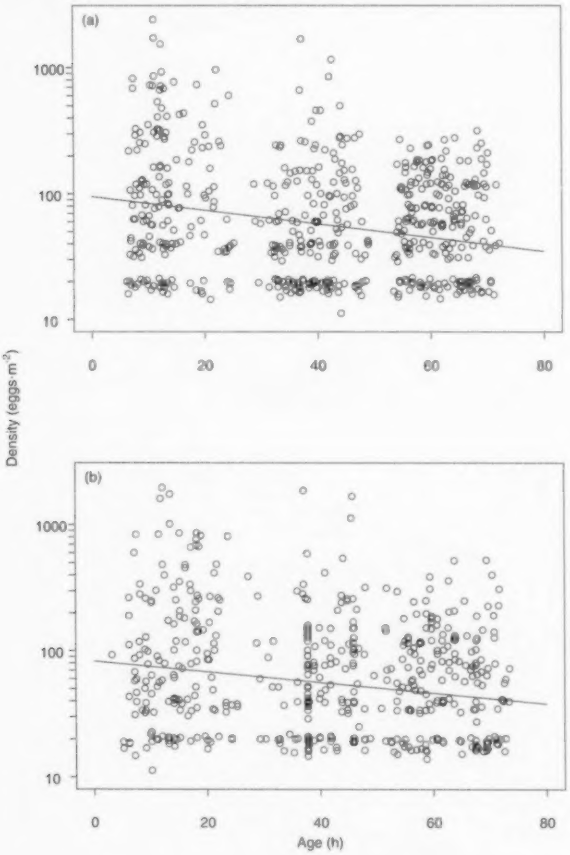


Table 1. Point and coefficient of variation (CV, %) estimates of daily egg production rates and mortality using both the traditional and new estimates of age and analytical and bootstrap procedures.

Method	Analytical estimates (point estimate (CV))	Bootstrap estimates (corrected point estimate (CV))
Traditional	D_0 = 82.85 (19.6)	D_0 = 81.86 (19.3)
	z = 0.0097 (46.4)	z = 0.0094 (46.8)
New	D_0 = 95.11 (17.7)	D_0 = 92.20 (19.2)
	z = 0.0125 (32.8)	z = 0.0115 (41.7)

Note: D_0 is in eggs·m^{-2}·day^{-1} and z in h^{-1}. Analytical procedures do not include ageing errors, whereas the bootstrap procedure using the new estimates of age does.

within the range of possible ages predicted by the stage-to-age model, and at the same time, the back-calculated spawning times from these resulting ages are within the daily spawning range predicted by the spawning times PDF. Thus, the two independent sources of information used have been incorporated in the ageing procedure in such a way that the resulting ages are coherent with both sources, but they are also more precise than the ages that could have been obtained from any of the two sources of information alone.

The ages obtained using the method proposed here are more realistic than the ones obtained using the traditional method, which relies on a very strong synchronicity assumption. In a natural population, one would expect the eggs to be spawned over a given period rather than instantaneous, synchronous release, so eggs from a given day-cohort will show a range of ages that should reflect the range of spawning times. This range of possible ages and the uncertainty in the ageing procedure that this natural variability produces should be incorporated in any posterior method that uses ages as a covariate. That is the case for the DEPM, in which daily egg production rates are calculated by fitting a mortality curve to the density of eggs classified in day-cohorts. The inclusion of the ageing error in the estimation of daily egg production rates can be obtained by resampling from the resulting ages produced by the new ageing method. In the example presented here, the inclusion of the ageing uncertainty in the estimation of the daily egg production rate produces an 8% increase in CV from the estimate in which no ageing errors were introduced. This increase is somehow masked by the large variability associated with some of the parameters of the mortality curve (as much as about 40% in the mortality rate). Nevertheless, other works in which additional covariates are used in the egg production rate estimation procedure (Borchers et al. 1997; Augustin et al. 1998; Bernal 1998) manage to reduce the variability associated with the model used to estimate the egg production rates, by using Generalized Additive Models (GAMs, Hastie and Tibshirani 1990). In those cases, the ageing uncertainty can account for a nontrivial percent of the total uncertainty, and obviating it can lead to significant bias in the variance estimation.

One of the important features of the ageing method presented here is the potential for using stage-to-age models and spawning times PDFs that reflect the biology of the studied species. There are three main requirements to apply the ageing method to any species. First, it is necessary that the species shows daily spawning synchronicity, otherwise the only information available for ageing comes from the stage-to-age models. Second, it is also necessary that each egg stage lasts less than a day, otherwise the range of ages for a given stage will be large enough to prevent the method from determining on which day the egg was spawned, and thus the errors associated with the ageing procedure will be too large. Third, it is necessary to have suitable models for both the spawning times PDF and the stage-to-age stochastic model to apply the general formulation of the ageing procedure. Of course, the better the knowledge about the species in the area of interest is, the better will be the performance of the ageing method.

The assumptions used to construct the spawning times and the stochastic stage-to-age model in our example are, in some cases, oversimplifications, because not enough information was available to construct adequate models based on empirical observations. The spawning times PDF has been based on prior knowledge of sardine biology from other parts of the world (Smith and Hewit 1985), adapted to Spanish sardine populations using findings by Pérez et al. (1989). Nevertheless, the agreement between the assumed PDF and the back-calculated spawning times from the stage-to-age model is good, which validates the assumed distribution of spawning events throughout the day. In any case, the spawning times PDF recreates a spawning behaviour that is more logical than either a uniform distribution of spawning times within a given spawning period or a single-event release of eggs in the day, and seems to fit the back-calculated spawning times from the stage-to-age model relatively well.

The stochastic version of the stage-to-age model has been constructed using a series of assumptions: a non-overlapping stage duration scheme, with durations defined by the midpoints of the stage intervals, and a uniform distribution of ages within each stage. There is not enough data to check the validity of the assumption of stage duration for all combinations of stages and temperature. Also, as mortality should affect the eggs in all stages, one would expect a decreasing number of eggs with increasing age within a stage, not a uniform distribution of eggs within a stage. Nevertheless, estimating stage- and temperature-dependent mortality is not easy. Thus, the mortality has been neglected in the ageing procedure. Although the duration of any stage in sardine is short, mortality in pelagic eggs is large, and so to obtain accurate measurements of errors in the ageing procedure, the validity of assumptions like this one should be checked, and if proved invalid, replaced with more appropriate ones. One interesting solution to improve the ageing procedure by introducing mortality within stages could be to iteratively estimate mortality from the resulting ages (as suggested above, from the results of the graphical method) and use the mortality function to generate a distribution of ages within stages. Again, it is important to note that mortality within stages has not been incorporated in the previous standard ageing procedure and at least, the new procedure creates a framework in which developments in this field can be incorporated easily in the method.

The method presented here provides a sensible way for incorporating information and assumptions about the biology of the studied species and can measure the error associated with the parameters of interest, given the models and assumptions taken. It allows the information to be used in different degrees of complexity. Thus, it can use the same information as that used by standard ageing methods like that of Lo (1985). Nevertheless, as it also allows the information to be introduced in more complex ways, via empirical or semi-empirical models, it is desirable that carefully designed experiments are carried out to precisely define the PDF of spawning times and the stage-to-age stochastic model for a given species and location, with the aim of obtaining more precise estimates of egg ages.

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Appendix 1. Notation used in the paper.

t, egg incubation temperature, also identified as survey temperature at 20-m depth.
τ, time of day.
τ_s, survey time.
N_{eggs}, number of surveyed eggs.
N_{stages}, number of stages of a given species. For sardine eggs, $N_{\mathrm{stages}} = 11$.
i, egg stage ($i = 1,\ldots,N_{\mathrm{stages}}$).
j, individual eggs caught in a survey ($j = 1,\ldots,N_{\mathrm{eggs}}$).
$a = a_j$, age of a given egg j.
$\bar{a}_{i,t}$, mean age of stage i eggs at temperature t.
$a_{\mathrm{initial},j}$, initial age of an egg j predicted by the stochastic stage-to-age model, to be introduced in the ageing procedure.
$a_{\mathrm{final},j}$, final age of an egg j obtained by the ageing procedure.
$a_{\mathrm{trad},j}$, age of an egg j, as obtained by the Lo (1985) ageing procedure.
θ, parameters of the deterministic stage-to-age model ($\theta = \theta_1,\ldots,\theta_n$). For the Lo model, $n = 4$.
$\varphi_{i,t}$, parameters defining the age range within stage i and temperature t for the stochastic stage-to-age model.
$g(a{:}\,i,t,\theta,\varphi_{i,t}) = g(i,\,t)$, general stochastic stage-to-age model.
$f(\tau;\beta) = f(\tau)$, general PDF of spawning times.
$f'(\tau) = \dfrac{f(\tau)}{\max(f(\tau))}$, scaled PDF of spawning times.

Changes in zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada

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Abstract: The crustacean zooplankton community of Harp Lake, Ontario, Canada, has changed appreciably since the invasion by the spiny water flea, *Bythotrephes*. Crustacean species richness has declined, large-bodied Cladocera have replaced small-bodied ones, and there has been a downward trend in the total abundance of zooplankton because copepod abundance has remained stable while Cladoceran abundance has declined. Although the zooplankton community has now been stable for 4 years (1995–1998), the biology of the invader has changed dramatically. In particular, there have been 10-fold differences in the mean annual abundance of *Bythotrephes* in this 5-year period and substantial changes in the timing of population maxima. We attribute these changes to two factors: (*i*) transition from a summer to a fall switch from parthenogenesis to gametogenesis and (*ii*) interannual differences in the thickness of a warm, dark stratum in the lake. We hypothesize that this stratum provides a refuge for *Bythotrephes* from predation by lake herring, *Coregonus artedii*.

Résumé : La communauté des crustacés du zooplancton du lac Harp, en Ontario, Canada, s'est modifiée de façon notable depuis l'invasion de la Puce d'eau épineuse, *Bythrotrephes*. La richesse en espèces des crustacés a décliné. Les cladocères de grande taille ont remplacé ceux de petite taille et il y a une tendance à la baisse dans l'abondance totale du zooplancton, car, bien que la densité des copépodes soit demeurée constante, celle des cladocères a baissé. La communauté zooplanctonique est restée stable depuis 4 ans (1995–1998); néanmoins, la biologie de l'espèce envahissante a changé de façon spectaculaire. En particulier, il y a eu des variations par un facteur de 10 des densités annuelles moyennes de *Bythotrephes* pendant cette période de 5 ans et des changements importants dans la phénologie des maximums de densité. Nous attribuons ces changements à deux facteurs : (*i*) un déplacement de l'été à l'automne du passage de la parthénogenèse à la gamétogenèse et (*ii*) aux différences inter-annuelles de l'épaisseur d'une strate obscure et chaude dans le lac. Nous croyons que cette strate fournit un refuge à *Bythotrephes* contre la prédation exercée par le Cisco de lac, *Coregonus artedii*.

[Traduit par la Rédaction]

Introduction

The population dynamics of introduced species are difficult to predict. "Boom and bust" dynamics are common for both introduced plants (Creed and Sheldon 1995) and animals (Williamson and Fitter 1996), but monotonic increases to steady states (Ramcharan et al. 1992) are also common. The dynamics of particular invaders may be system-specific. For example, Ramcharan et al. (1992) noted both boom–bust dynamics and monotonic increases in abundances in invading zebra mussel populations. Hence, we cannot reliably predict the long-term demographics of introduced species in particular systems either from short-term studies in those systems or from longer-term studies in other invaded habitats.

The cladoceran *Bythotrephes longimanus* (Crustacea: Branchiopoda: Onychopoda), until recently termed *B. cederstroemi* (Grigorovich et al. 1998), invaded each of the Laurentian Great Lakes in the 1980s. The probable source was the Baltic Sea, a population originating in Lake Ladoga, upstream of St. Petersburg (Berg et al. 2001). *Bythotrephes* first appeared in Canadian Shield lakes in 1989 (Yan et al.

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1992). We predict that it will become an important member of the Shield lake plankton for three reasons. Firstly, the invader is spreading rapidly. Since 1989, *Bythotrephes* has colonized at least 34 inland lakes in Ontario (MacIsaac et al. 2000). Secondly, many Shield lakes have suitable *Bythotrephes* habitat, given its apparent preference for large, oligotrophic lakes in its native Eurasia (MacIsaac et al. 2000). Finally, *Bythotrephes* has had large impacts on the structure of zooplankton communities (Lehman and Caceres 1993; Yan and Pawson 1997) soon after its establishment. Unfortunately, the available North American *Bythotrephes* case studies are too brief to determine if the invader has characteristic demographics or if the effects of the invader are permanent. Both European (Manca and Ruggiu 1998) and North American Great Lakes' studies (Johannsson et al. 1991) indicate that *Bythotrephes* populations are characterized both by large interannual variations in abundance and by flexible demographic and behavioural responses to predators (Bilkovic and Lehman 1997; Straile and Hälbich 2000). Hence, we should not assume that the patterns in zooplankton detected soon after North American *Bythotrephes* invasions will be stable.

Bythotrephes first appeared in Harp Lake, Ontario, Canada, in 1993 (Hall and Yan 1997). By 1995, the crustacean zooplankton of the lake had changed in several ways. The abundance of two small taxa, *Bosmina longirostris* and *Tropocyclops extensus*, declined appreciably, and three small cladocerans, *Chydorus sphaericus*, *Diaphanosoma birgei*, and *Bosmina* (*Neobosmina*) *tubicen*, disappeared from our collections. In contrast, the abundance of a few larger taxa, *Holopedium gibberum* and especially *Daphnia mendotae* and *Leptodiaptomus sicilis*, increased to previously unrecorded levels (Yan and Pawson 1997). Eliminating competing hypotheses, Yan and Pawson (1997) suggested that *Bythotrephes* was responsible for these changes. Dumitru et al. (2000) provided supporting evidence, demonstrating that despite substantial predation from lake herring (Coulas et al. 1998), the *Bythotrephes* population in Harp Lake consumed all, and occasionally even more than all, of the productivity of crustacean zooplankton in the lake during the summer of 1995.

We now suspect that the interactions quantified by Dumitru et al. (2000) between *Bythotrephes* and its Harp Lake prey might have been short-lived. After all, *Bythotrephes* growth was unusual in 1995. *Bythotrephes* typically grow between each instar (e.g., Burkhardt 1994; Straile and Hälbich 2000), but there was no growth between instars II and III in Harp Lake in the summer (Yan and Pawson 1998). The life history of *Bythotrephes* was also unusual. *Bythotrephes* normally switches from parthenogenetic to gametogenic reproduction in the fall (Straile and Hälbich 2000), but this switch happened in midsummer in Harp Lake in 1994 and 1995. Yan and Pawson (1998) hypothesized that these peculiarities in demographics were attributable to a scarcity of prey in midsummer, an observation supported by Dumitru et al. (2000). Here, our goal is to determine if the *Bythotrephes* population or its zooplankton prey changed after 1995. In particular, our objectives are to determine (*i*) if the short-term changes in the zooplankton community observed by Yan and Pawson (1997) have been maintained, if any new changes have developed, and if the Harp Lake changes are unusual in comparison with neighboring lakes that have not been invaded; (*ii*) if the unusual life-history characteristics of *Bythotrephes* observed by Yan and Pawson (1998) have been maintained; and (*iii*) if there is evidence that a refuge from lake herring predation is important in the demographics of *Bythotrephes* in Harp Lake, as suspected by Yan and Pawson (1998).

Materials and methods

Study lake descriptions

Harp Lake is a single-basin, relatively small (71.4 ha), deep (z_{max} of 37.5 m) lake located in southcentral Ontario, Canada. Its waters are soft and nutrient-poor (Table 1), as is typical of the region. Before the arrival of *Bythotrephes*, an average of 16 crustacean zooplankton taxa was recorded each year in the lake (Yan and Pawson 1997). Copepods contributed roughly 80% of the biomass. Because the hypolimnion of the lake is both deep and well oxygenated, several of these were cold stenotherms and (or) glacial relicts, including *Epischura lacustris*, *Leptodiaptomus sicilis*, and *Senecella calanoides*. *Coregonus artedii*, lake herring, is the dominant pelagic zooplanktivorous fish in the lake (Coulas et al. 1998). *Bythotrephes* first appeared in this region of Ontario in 1989 (Yan et al. 1992). It first appeared in zooplankton samples in Harp Lake in the summer of 1993, having perhaps invaded a year or two earlier.

We compare the changes in the zooplankton of Harp Lake, associated with the arrival of Bythotrephes, with those in the neighbouring Blue and Red Chalk lakes, which have not been colonized by Bythotrephes. Like Harp Lake, the two reference lakes are nonacidic, oligotrophic, clear-water, stratified lakes (Table 1) with largely forested catchments. Yan et al. (1996) describe their zooplankton communities.

Sampling and sample enumeration

Each time that we visited Harp Lake, we estimated the euphotic zone depth as twice the Secchi depth. We also quantified thermal stratification using a temperature profile taken at 1-m intervals at the deepest spot in the lake. We identified the top of the hypolimnion as the depth at which the decline of temperature with depth fell to $<1°C \cdot m^{-1}$.

Yan and Pawson (1997) detail the methods used for locating the one sampling station and for collecting, identifying, measuring, and counting crustacean zooplankton from Harp Lake between 1978 and 1995. We used identical methods between 1996 and 1998 in Harp Lake and in all years in Blue Chalk and Red Chalk lakes (Yan et al. 1996). Yan and Pawson (1998) detail the methods using for locating the 10 *Bythotrephes* sampling stations in Harp Lake and for collecting *Bythotrephes* in 1994 and 1995. They also detail methods that were used to assess the gender, developmental stage, fecundity, stage of brood development, and clutch size of parthenogenetic and gametogenic broods. We used identical methods for collecting and counting *Bythotrephes* from 1996 to 1998 with the following exceptions. The filtration efficiency of the *Bythotrephes* net (0.75 m diameter, 2.5 m long, 285 μm mesh) averaged 88% between 1995 and 1997. Efficiency was not measured in 1988; the 1995–1997 mean value was employed instead. Vertical hauls were taken from 2 to 3 m above bottom to the surface at all 10 stations in all years except 1996, when samples were collected only from the four stations within the 21-m contour and only from the bottom of the metalimnion.

Most samples were examined in their entirety for *Bythotrephes*. We examined 550, 1144, 30, 237, and 1641 *Bythotrephes* annually from 1994 to 1998, respectively. Gender was not assessed in 1996 or 1997.

Table 1. Limnological comparison of Harp, Blue Chalk, and Red Chalk lakes.[a]

	Harp Lake	Blue Chalk Lake	Red Chalk Lake
Latitude	45°23′	45°12′	45°11′
Longitude	79°07′	78°56′	79°56′
Lake area (ha)	71.4	52.4	57.1
Mean depth (m)	13.32	8.5	14.2
Maximum depth (m)	37.5	23	38
Total phosphorus ($\mu g \cdot L^{-1}$)	6.78	5.97	5.27
pH	6.27	6.6	6.30
Secchi depth (m)	3.98	6.56	5.95
Conductivity (μS)	35.7	28.6	28.8

[a] Long-term average of annual means from 1975 to 1999 (K. Somers, Ontario Ministry of Environment, Dorset, Ont., unpublished data).

Hall and Yan (1997) noted that only 2% of the *Bythotrephes* population was located in the hypolimnion during the day in Harp Lake; hence, we report *Bythotrephes* abundance per unit volume of epilimnion + metalimnion. *Bythotrephes* abundance did not differ among the nine sampling strata when tested in 1994 and again in 1998; hence, we report the descriptive statistics of the population without correcting for the areas of the sampled strata.

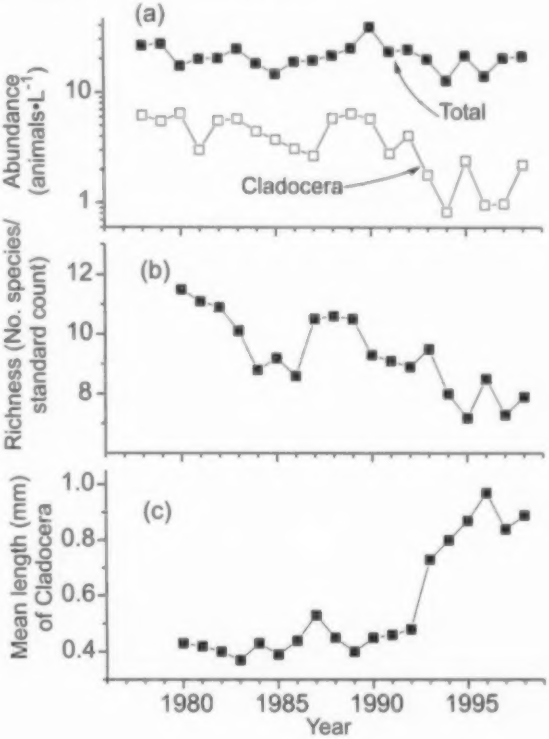
Analytical methods

We can be certain that *Bythotrephes* was in Harp Lake in 1993. Hence, for statistical comparisons, we treat 1993 to 1998 as the postinvasion period. All statistical analyses were performed on ice-free season averages. We used several univariate metrics, including total zooplankton abundance (log-transformed), average species richness, i.e., the average number of species recorded in our standardized counts of roughly 250 animals, and the size of all Cladocera measured in the year. To test if the community changed after the arrival of *Bythotrephes*, we calculated a t statistic assuming unequal variances, given the unbalanced design (15 preinvasion and 6 postinvasion years). If significance levels were close to 0.05 in this conventional assessment, we retested the significance of the t statistic using a randomization procedure, i.e., by reshuffling the time series 999 times and recalculating the difference between means of the last six shuffled data points in comparison with the mean of previous data points in the series. This approach was used because our time series of annual means should not be considered a random sample, and it is unbalanced, implying some risk of bias in the use of conventional statistical tables (Manly 1991). Because multivariate metrics may provide more sensitive indications of change in communities than do univariate ones (Yan et al. 1996), we also described changes in average community composition in the lake using the correspondence analysis routines in Statistica. We used the same 17 zooplankton taxa previously used by Yan and Pawson (1997), with log-transformed, ice-free season mean abundances of these taxa as our input.

Results

The zooplankton community of Harp Lake has changed dramatically since the arrival of *Bythotrephes* in 1993. However, there have been no substantial changes in the community since the 1995 field season, i.e., since Dumitru et al. (2000) predicted transitions in the zooplankton community and (or) in the *Bythotrephes* population.

Fig. 1. Long-term changes in (*a*) total and Cladoceran zooplankton abundance, (*b*) crustacean species richness, and (*c*) mean Cladoceran body length in Harp Lake between 1978 and 1998. *Bythotrephes* was first detected in 1993.



With only 3 years of postinvasion data (1993–1995), Yan and Pawson (1997) were not able to detect a change in the overall abundance of zooplankton in Harp Lake; however, this now appears to be changing. The geometric mean of the mean annual zooplankton abundances fell from 22.1 animals·L^{-1} (s^2 = 1.02, n = 13) before the arrival of *Bythotrephes* to 18 animals·L^{-1} (s^2 = 1.02, n = 6) between 1993 and 1998 (Fig. 1*a*). This change in mean total crustacean zooplankton abundance, while not significant at $p = 0.05$ ($t = 1.83$, $p = 0.096$ by conventional assessment, and $t = 1.86$, $P = 0.075$ with 999 randomizations, after log-transformation), does suggest a trend. This trend was entirely attributable to a significant decline in the mean abundance of Cladocera (log-transformed) after 1992 ($t = 5.6$, $p < 0.001$), not to any change in the abundance of Copepoda (Fig. 1*a*).

There is no doubt about the changes in overall crustacean species richness and size structure. Zooplankton richness has declined in Harp Lake since the arrival of *Bythotrephes* (Fig. 1*b*). The average number of species detected in our standard counting protocol was 9.92 species per count between 1980 and 1992. It fell by 18% to a mean of 8.1 species per count in the 6 years after *Bythotrephes* was detected ($t = 4.18$, $p < 0.001$ with 999 randomizations). The mean individual body length of Cladocera in our samples doubled from 0.43 mm before the invasion to 0.85 mm after the invasion (Fig. 1*c*, $t = 11.7$, $p < 0.001$ after 999 randomizations).

The change in mean Cladoceran size was principally attributable to a change in the relative abundances of different

Fig. 2. Long-term changes in the ice-free season mean abundances of all common zooplankton species in Harp Lake. Note that the species are ordered from top left to bottom right based on their scores on CA axis I (see Fig. 4).

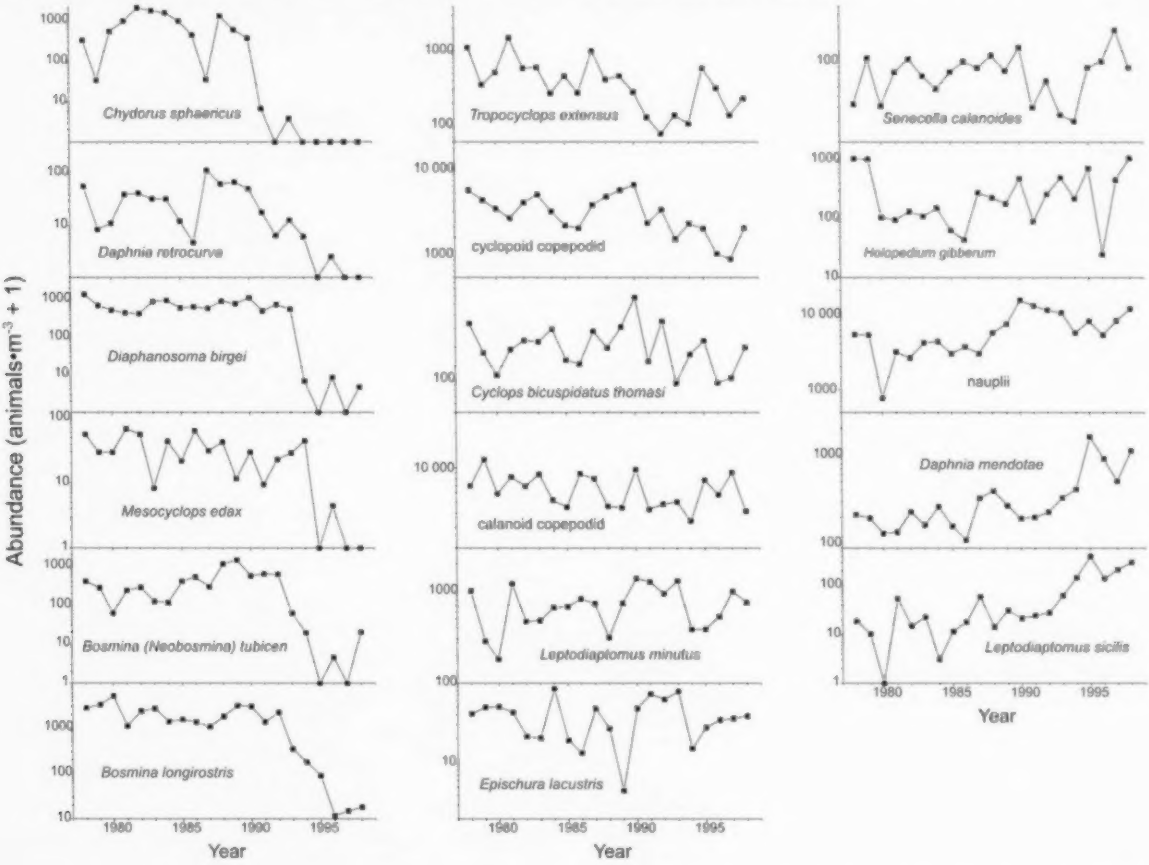
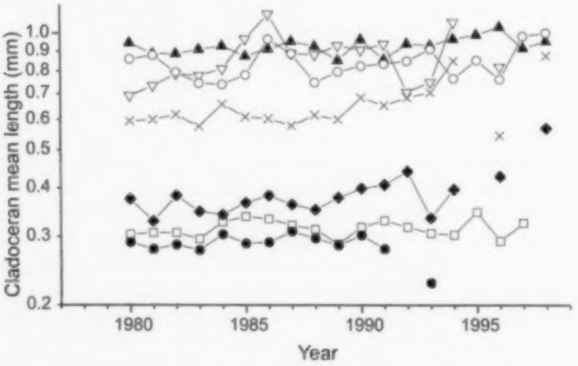


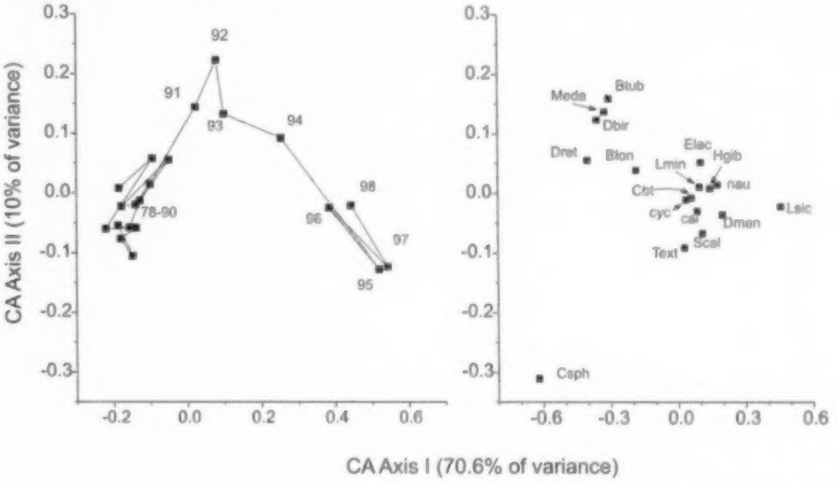
Fig. 3. Long-term changes in the mean annual body lengths of Cladoceran taxa in Harp Lake. The taxa are *Bosmina longirostris* (□), *Chydorus sphaericus* (●), *Daphnia mendotae* (▲), *Daphnia retrocurva* (▽), *Bosmina (Neobosmina) tubicen* (◆), *Holopedium gibberum* (○), and *Diaphanosoma birgei* (×). The length of *H. gibberum* has been corrected for shrinkage in formalin.



zooplankton species in the lake rather than to a change in size of individual species. The abundance of mostly small Cladocera decreased by orders of magnitude (Fig. 2). These included *Chydorus sphaericus* (long-term mean length of 0.29 mm in Harp Lake), which declined in abundance in 1991, before we had actually detected Bythotrephes in the lake, *Daphnia retrocurva* (0.86 mm), *Diaphanosoma birgei* (0.65 mm), *Bosmina* (*Neobosmina*) *tubicen* (0.39 mm), and *Bosmina longirostris* (0.31 mm). In contrast, the abundance of the two larger Cladocerans, *Holopedium gibberum* (0.84 mm) and *Daphnia mendotae* (0.93 mm), has increased appreciably. There were no long-term changes in the mean sizes of individual cladoceran taxa if we ignore some recent artifactual increases in variability of the size of those species with plummeting populations (Fig. 3). Hence, it is clear that the cause of the overall increase in Cladoceran size in the lake (Fig. 1*c*) was the replacement of small taxa with larger taxa after 1993.

These enormous changes in the zooplankton community of Harp Lake were complete by 1995. There were no appearances, disappearances, or appreciable changes in the abundance of taxa between 1995 and 1998 (Fig. 2). Hence, there were no appreciable changes in abundance, richness, or

Fig. 4. A scattergram of first and second axis scores of a correspondence analysis of the mean annual abundances of 17 common zooplankton species (see Fig. 2) in Harp Lake. The left-hand plot locates the year scores in ordination space, years with similar community composition being near neighbours. The right-hand plot locates the taxa in ordination space, namely *Bosmina* (*Neobosmina*) *tubicen* (Btub), *Bosmina longirostris* (Blon), calanoid copepodids (cal), cyclopoid copepodids (cyc), *Chydorus sphaericus* (Csph), *Cyclops bicuspidatus thomasi* (Cbt), *Daphnia mendotae* (Dmen), *Daphnia retrocurva* (Dret), *Diaphanosoma birgei* (Dbir), *Epischura lacustris* (Elac), *Leptodiaptomus minutus* (Lmin), *Leptodiaptomus sicilis* (Lsic), nauplii (nau), *Senecella calanoides* (Scal), and *Tropocyclops extensus* (Text). Note the different *x*-axes lengths.



size structure of the community since 1995 (Fig. 1). Further, the correspondence analysis confirms that the community had two periods of compositional stability separated by a transition in the early 1990s (Fig. 4).

Although there have been no appreciable recent changes in the crustacean zooplankton assemblage in Harp Lake, the situation for *Bythotrephes* is quite different. Patterns of abundance, growth, and life history have changed both within and among years.

The abundance patterns of *Bythotrephes* have changed since 1995 in several ways. The mean abundance of *Bythotrephes* for the ice-free season was 2 animals·m^{-3} in 1994 and 3.2 m^{-3} in 1995. In both years, the population was very small in the spring, lagging well behind increases in water temperature and population increases of small Cladocera (Yan and Pawson 1998). The *Bythotrephes* population then reached a single maximum in July, after which it fell in response to a switch from parthenogenesis to gametogenesis and resting-egg production. The only similarity to this 1994–1995 pattern in recent years is the low population size in the spring (Fig. 5). All else has changed. In 1996 and 1997, the population was small at all times, averaging only 0.26 and 1.32 animals·m^{-3}, respectively. At 5.14 m^{-3}, the population was larger in 1998 than in any other year. The interannual changes in seasonality were dramatic. The summer maximum of 1994 and 1995 disappeared to be replaced by an unprecedented fall maximum in 1998.

The summer maximum failed to appear from 1996 to 1998 despite good aestival fecundity. During July and August, the average sizes of parthenogenic clutches were quite similar between 1994 and 1998 at around 3 embryos per clutch (Fig. 6). Further, the number of gravid animals was similar, so that the summer egg ratio was similar in 1995 (at 0.24 eggs·female^{-1}) and in 1998 (at 0.36). The persistence of the population into the fall of 1998 suggests a major change from the earlier life-history pattern in the lake. Indeed, in comparison with 1994 and 1995, there were far fewer males in midsummer in 1998 (Fig. 7*a*). Of greater importance, no females were producing clutches of resting eggs in July and early August of 1998, whereas most females had switched to resting-egg production in the summers of 1994 and 1995 (Fig. 7*b*).

Growth patterns of *Bythotrephes* also changed during our study. In 1995, there was very little growth between instars II and III in the summer, and body sizes actually fell through August (Fig. 8). In contrast, in 1998, mean lengths increased from instar II to III at all times, and the body size of each instar increased almost continuously throughout the year.

Discussion

Yan and Pawson (1997) detected a change in the richness of the zooplankton community of Harp Lake after the *Bythotrephes* invasion but did not report a change in mean Cladoceran size or abundance. Our addition of 3 years to the time series confirms that the richness of the community has indeed fallen. We supplement the previous work with our evidence that total abundance of zooplankton appears to be declining in the lake in response to a large drop in Cladoceran abundance.

Although reductions in total zooplankton abundance have been observed in mesocosm experiments with *Bythotrephes* (Wahlström and Westman 1999), our observation of a reduction in the abundance of an entire natural zooplankton community appears to be novel. There certainly have been reports of dramatic alterations in the daphniid component of

Fig. 5. Seasonal changes in the mean (± standard error) abundances of *Bythotrephes* in the epilimnion + metalimnion of Harp Lake from 1994 to 1998 (Figs. 5*a* to 5*e*, respectively).

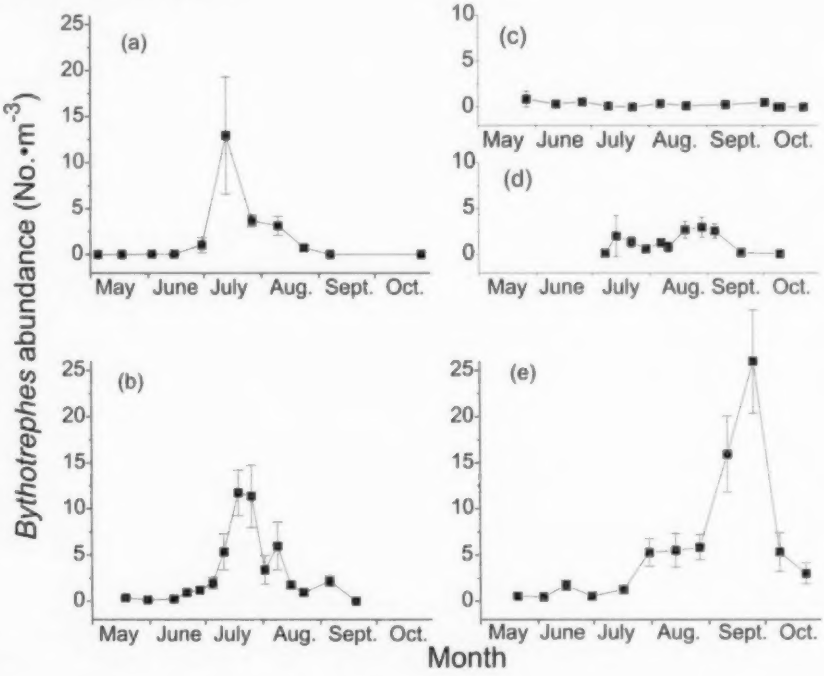
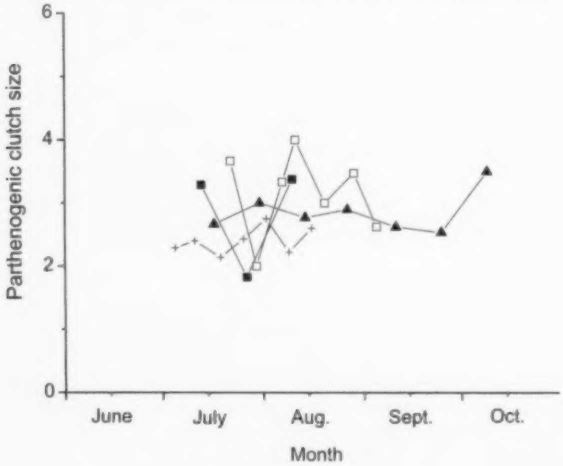


Fig. 6. Seasonal changes in the size of parthenogenic clutches of *Bythotrephes* in Harp Lake in 1994 (■), 1995 (+), 1997 (□), and 1998 (▲). Dates where <3 clutches could be sized are excluded.

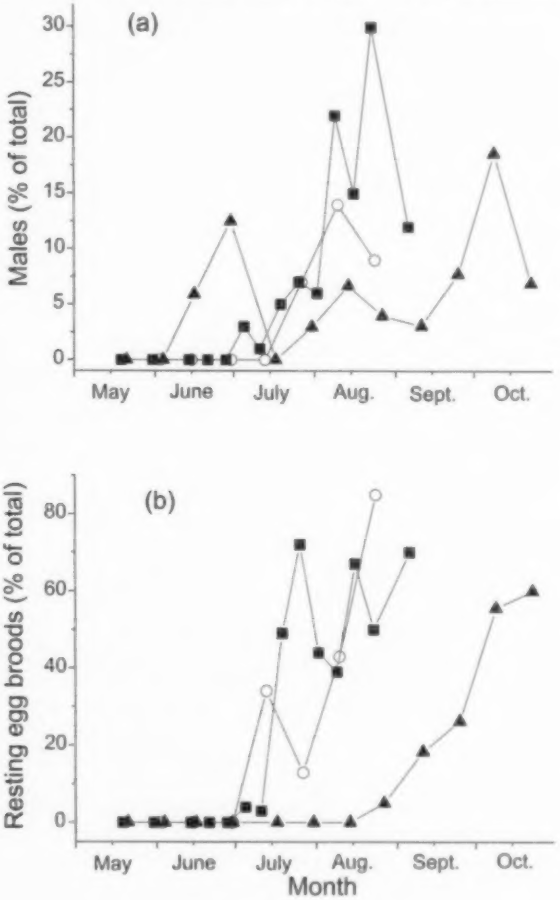


the Cladoceran assemblage (Manca and Ruggiu 1998; Lehman and Caceres 1993) but apparently not for the total zooplankton assemblage. If we are to attribute this change in Harp Lake to the arrival of *Bythotrephes*, we must, as a minimum, prove both that the observed changes are unusual in magnitude for the region and that synchronous changes have not occurred in nearby uninvaded lakes. Such interlake synchrony has been observed for some zooplankton species, e.g., *Leptodiaptomus minutus*, in other lakes in the region (Rusak et al. 1999) and attributed to annual variations in climate. Hence, it is possible that the decline in zooplankton abundance detected in Harp Lake, although real, may have had nothing to do with the arrival of *Bythotrephes*.

The decline in species richness observed is unprecedented in nonacidifying lakes on the Shield (Arnott et al. 1999); however, we have no readily available published data to compare with the changes in mean Cladoceran size and total zooplankton abundance. Hence, we compared these long-term changes in Harp Lake with those in Blue Chalk and Red Chalk lakes. The reference lake comparisons support our conclusion that Cladoceran size and total zooplankton abundance have changed in Harp Lake as a result of the invasion, not as a result of a regional climatic anomaly. Although mean zooplankton abundance in Harp Lake declined after 1992, there was no change in mean annual abundance in Blue Chalk Lake (t = 0.66, p = 0.52, tested on log-transformed data) or in Red Chalk Lake (t = –1.53, p = 0.16) after 1992 (Fig. 9*a*). Hence, the decrease in mean zooplankton abundance observed in Harp Lake was not a pattern found across the region. No formal analysis is required to determine that the increase in Cladoceran body size observed after 1992 in Harp Lake was unusual in comparison with the reference lakes (Fig. 9*b*). Hence, we conclude that the zooplankton community of Harp Lake changed after 1992 for reasons peculiar to the lake. We hypothesize that the arrival of *Bythotrephes* is this peculiarity.

Although the zooplankton community has not changed appreciably since 1995, the *Bythotrephes* population certainly has. The change in seasonality cannot be explained by exam-

Fig. 7. Seasonal changes in 1994 (○), 1995 (■), and 1998 (▲) of (*a*) males, as percent of the total *Bythotrephes* population, and (*b*) the percent of the total broods produced by *Bythotrephes* that were resting-egg broods. Too few animals were caught in 1996 for the sex ratio assessment, and gender was not recorded in 1997. The small, late-June peak in 1998 in Fig. 7*a* represents only one animal.



ining the demographics of *Bythotrephes* itself. If the seasonality of *Bythotrephes* in Harp lake was responding solely to its inherent biology, there should have been a large population in the summer of 1998. After all, fecundity was the same as in earlier years but far more females were reproducing parthenogenetically. As the summer population was actually relatively small in 1998, there must have been a dramatic increase in mortality to offset the increased natality. Fish predation is the most likely source of this extra mortality.

Lake herring is the principal pelagic planktivorous fish in Harp Lake, and *Bythotrephes* is its preferred prey. Coulas et al. (1998) examined the diet of lake herring in Harp Lake on seven occasions in 1995 and noted that lake herring selected Bythotrephes over four other prey categories on every date, with the highest selection evident when *Bythotrephes* populations peaked. Yan and Pawson (1998) estimated the vulnerability of *Bythotrephes* to lake herring predation as the

Fig. 8. Seasonal changes in the body + head length of female *Bythotrephes* (± standard error (SE)) in Harp Lake in (*a*) 1995 and (*b*) 1998. These years were selected given their large sample size. Instar IV animals are present only in the spring. Very few were captured; hence, their estimates are poor. Instars: I (■), II (○), III (◆), IV (*).

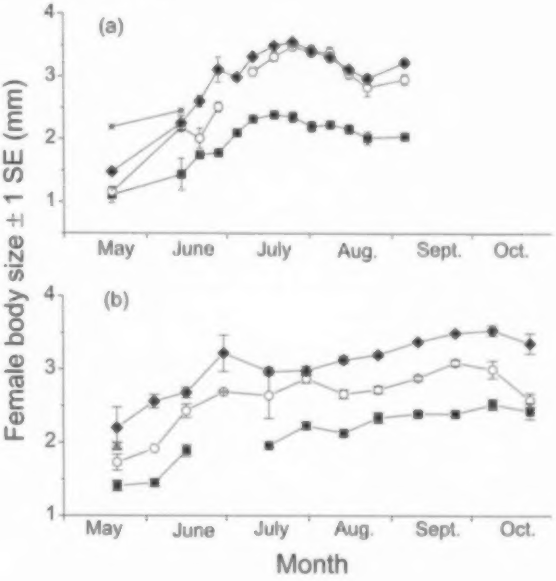


Fig. 9. Comparison of long-term changes in (*a*) the total crustacean abundance and (*b*) Cladoceran body length of zooplankton in Harp Lake (▲) with two noninvaded reference lakes, Blue Chalk Lake (□), and the main basin of Red Chalk Lake (○).

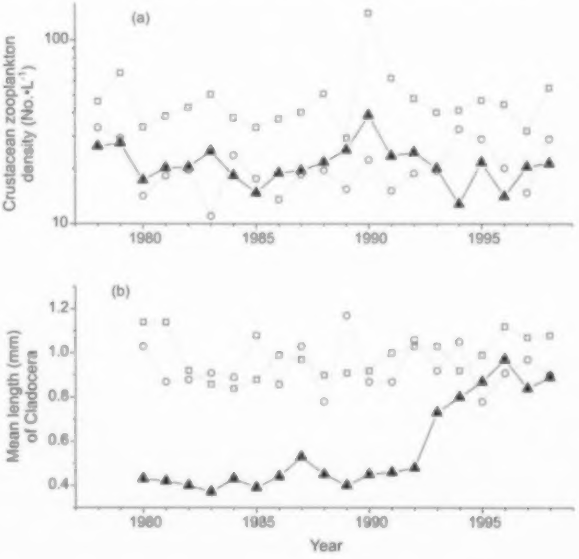


Fig. 10. Comparison of seasonal changes from 1993 to 1998 (Figs. 10*a* to 10*f*, respectively) in the presence and size of the refuge of *Bythotrephes* from predation by lake herring, i.e., the difference between the depth at the top of the hypolimnion and twice the Secchi depth. Positive values indicate the presence of the refuge, i.e., warm dark water.

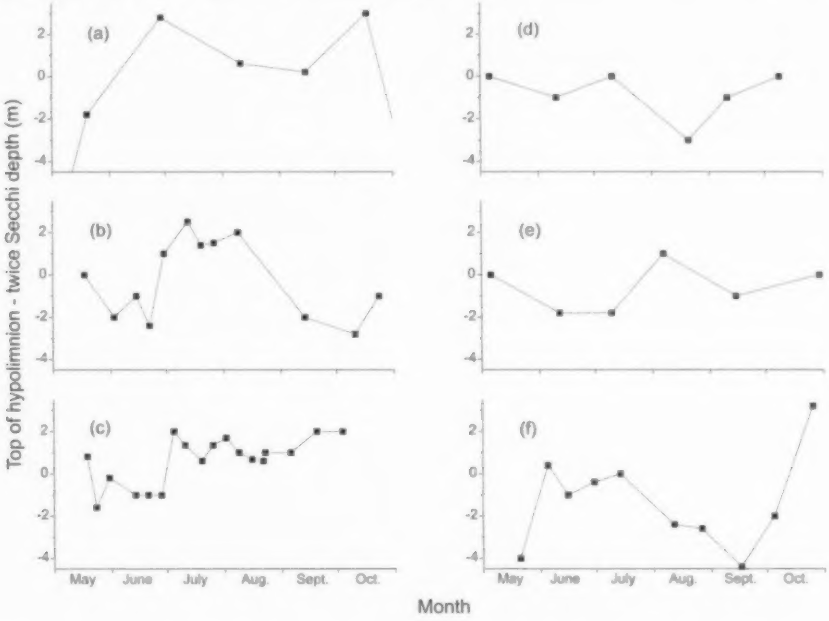
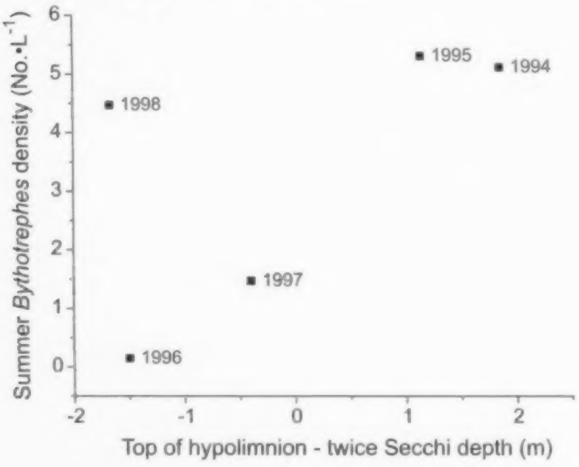


Fig. 11. Scattergram of mean abundance of *Bythotrephes* in Harp Lake in July and August (called "summer") vs. the summer mean of the refuge indicator (see Fig. 10).



difference between the depth at the top of hypolimnion and the euphotic zone depth (estimated as twice the Secchi depth, see their fig. 8). Where the euphotic zone includes some of the hypolimnion, the metric is negative, the mixed waters of the lake are well illuminated, and the risk of predation by the hypolimnetic lake herring was assumed to be high. When the top of the hypolimnion was deeper than twice the Secchi depth, a warm, dark layer existed which was hypothesized to offer *Bythotrephes* a refuge from predation on the assumption that lake herring would only leave their preferred hypolimnetic habitat (Coulas et al. 1998) if epilimnetic prey were visible.

We suggest that the long-term changes in summer population size of *Bythotrephes* in Harp Lake can be explained by two factors: changes in the availability of the refuge from lake herring predation and changes in *Bythotrephes* life history. This refuge was both thick and long-lasting in 1993, the first year that *Bythotrephes* appeared in our zooplankton samples (Fig. 10). We suggest that this presented an ideal situation for the new colonists to prosper in the lake. As noted by Yan and Pawson (1998), the refuge did not exist in the spring of 1994 or 1995. It was available in July and August of 1994 and 1995 but not in the summers of 1996 through 1998. The mean abundance of *Bythotrephes* in July and August was correlated with the thickness of refuge between 1994 and 1997 (Fig. 11), the thicker the warm dark layer, the more abundant the *Bythotrephes* ($r = 0.97$, $n = 4$, $p < 0.05$) in the summer. However, 1998 does not fit the pattern. In comparison with the previous 4 years, there are too many *Bythotrephes* given the absence of the hypothesized predation refuge. We suggest that the risk of predation fails to predict summer *Bythotrephes* population size in 1998 because the invader's life history changed in that year. Clutch sizes and egg ratios were similar in the summer, but unlike in earlier years, all of the summer clutches were parthenogenic in 1998.

Changes in body size are consistent with the hypothesis that predatory mortality varies among years. Instar II and III animals were smaller in the summer of 1998 than in 1995, suggesting increased size-selective predation by lake herring (Bilkovic and Lehman 1997; Coulas et al. 1998).

We cannot explain the change from aestival to autumnal resting-egg production in the lake. However, it is worth noting that the current pattern, the autumnal switch, is the typical one in Eurasia. It was the aestival switch of 1994 and 1995 that was the unusual pattern. It is possible that one strategy of the invader for coping with the multiple, novel cues in a new environment is early resting-egg production. Certainly, aestival resting-egg production has been interpreted as a stress response in other Cladocera (Arts and Sprules 1987), and Panov et al. (2000) recorded aestival resting-egg production in the invading fish-hook water flea, *Cercopagis pengoi*, in the Neva Estuary of the Baltic Sea.

It is clear that short data series collected soon after colonization are not adequate to quantify *Bythotrephes* abundance or typify *Bythotrephes* demographics. There was a great deal of interannual variability in demographics in Harp Lake. Similarly, *Bythotrephes* peak in Lake Ontario only in poor alewife years (Johannsson et al. 1991). We should not be surprised if single stable endpoints between *Bythotrephes* and their predators or prey do not develop.

There has been a substantial recent increase in interest in the study of nonindigenous species. We now know that the economic cost of such species is enormous (Pimental et al. 2000) and that they can fundamentally change the structure and functioning of food webs (Vander Zanden et al. 1999). Furthermore, more invasions will certainly occur. Major invasion corridors remain open and transport mechanisms remain active (Carlton and Geller 1993). Intentional introductions are still being planned (Ewel et al. 1999; Dextrase and Coscarelli 2000). Finally, a changing climate (Dukes and Mooney 1999) and the increased internationalization of trade (Buckingham 1998) foster the global spread of species.

Given the magnitude of this issue, our lack of understanding of the current impacts and the future risks of nonindigenous species is alarming. We must re-evaluate long-held notions about the factors that render habitats vulnerable to invaders (Lozon and MacIsaac 1997). We must build tools that can be used to predict the capacity of biota to survive transport, successfully colonize, and, finally, alter their new communities to the point that they become "nuisances" (Ricciardi et al. 1998). If we exclude the zebra mussel (Strayer et al. 1996), we have little of the information needed to build such tools for any freshwater invaders (Ojaveer et al.[2]). Our Harp Lake work suggests that such information cannot be developed quickly. Nonetheless, the importance of the task indicates we should begin developing this information, taking every opportunity to exploit existing long-term or large-scale data sets for the head start to understanding that they provide.

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Individual-based yield-per-recruit analysis, with an application to the Atlantic sea scallop, *Placopecten magellanicus*

Deborah R. Hart

Abstract: There can be considerable variation in fishing mortality risk among individuals in a stock, especially for sedentary or sessile species. An individual-based per-recruit model is proposed that can systematically deal with variability in fishing mortality among recruits. These variations can alter the yield per recruit (YPR) and biomass per recruit (BPR) that would be predicted from conventional theory. Where the YPR curve is concave, standard theory will tend to overestimate YPR, whereas the opposite will be true where the YPR curve is convex. Additionally, variations in fishing mortality among individuals can create a mismatch between conventional metrics of mean fishing mortality and that required to properly apply standard per-recruit theory. The concept of "recruit-weighted" fishing mortality is introduced to deal with this problem. An application of the model to the Atlantic sea scallop, *Placopecten magellanicus*, is presented that demonstrates that standard per-recruit theory may often misrepresent true YPR and BPR.

Résumé : Il peut y avoir une variation importante du risque de mortalité due à la pêche parmi les individus d'un même stock, particulièrement chez les espèces sédentaires ou sessiles. On trouvera ici une modélisation "par recrue", basée sur l'individu, qui permet de traiter de la variabilité de la mortalité due à la pêche chez les recrues. Ces variations peuvent affecter la prédiction du rendement et de la biomasse par recrue (BPR) par les théories habituelles. Lorsque la courbe de rendement par recrue (YPR) est concave, la théorie standard tendra à surestimer le rendement par recrue; elle le sous-estimera lorsque la courbe est convexe. De plus, les variations de la mortalité due à la pêche d'un individu à l'autre peuvent générer un désaccord entre les métriques conventionnelles de la mortalité moyenne due à la pêche et celles qui sont requises pour l'application correcte de la théorie standard "par recrue". L'introduction du concept d'une mortalité due à la pêche pondérée par recrue permet de résoudre ce problème. L'application du modèle au Pétoncle géant, *Placopecten magellanicus*, démontre que la théorie standard peut souvent fausser les véritables valeurs de rendement et de biomasse par recrue.

[Traduit par la Rédaction]

Introduction

One of the key assumptions of conventional yield-per-recruit (YPR) theory (Beverton and Holt 1957; Gulland 1983; Quinn and Deriso 1999) is that all individuals in a stock have the same growth rates and mortality risks, or at the very least, the expected yield obtained from recruits with the mean growth and mortality rates is representative of the yield obtained from averaging over all recruits in the fishery. For mobile species that are fairly "well mixed", this assumption may be a reasonable approximation. On the other hand, high variation of fishing mortality rates within sessile stocks may cause difficulties when applying standard YPR theory.

To take one simple example, suppose (average) fishing mortality is maintained at $F_{\max}$, the point where optimal YPR is obtained. Suppose further that one portion of the stock is fished at a level F_1 that is below $F_{\max}$, while the other is fished at a level F_2 above $F_{\max}$ (see Fig. 1). The resulting average YPR that would be obtained in this case would clearly be less than that obtained if all recruits had the identical fishing mortality risk $F_{\max}$, as would be assumed in conventional YPR theory.

The above example is a demonstration of a general mathematical result known as Jensen's inequality (see, e.g., Feller 1966; Ruel and Ayres 1999). In the present context, Jensen's inequality implies that if the fishing mortality risks of all recruits are less than the point of inflection c indicated in Fig. 1, so that they all lie in the region where the YPR curve is concave (down), then the YPR, when averaged over all recruits, is less than the yield of an "average" recruit that suffers the mean fishing mortality. In other words, in this situation, conventional YPR analysis would always overestimate the actual YPR that would be obtained when there is variation in individual fishing mortality risk. The degree of this overestimation depends on the amount of nonlinearity (i.e., the magnitude of the second derivative) of the YPR curve; it will be high where the nonlinearity is pronounced, and less substantial where the curve is nearly linear. If, instead, the fishing mortality risks of all recruits are larger than c, and so are in the region where the YPR curve is

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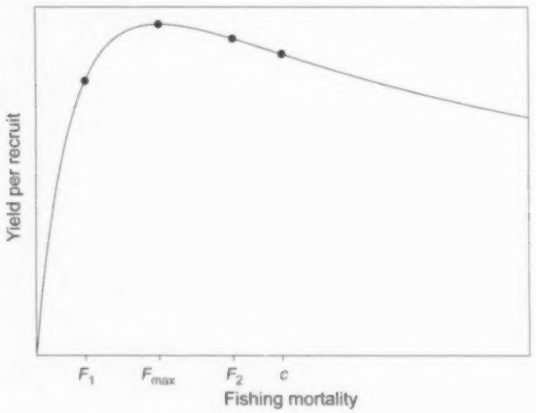
Fig. 1. Yield-per-recruit (YPR) curve indicating the fishing mortality producing maximal yield ($F_{\max}$), example fishing mortalities F_1 and F_2, which average to $F_{\max}$, and the inflection point *c*. The yields produced by these four fishing mortalities are indicated by the circles on the graph.



convex, then Jensen's inequality implies that standard per-recruit theory would underestimate the mean YPR averaged over all recruits.

Variations of fishing mortality risks among individuals may also cause difficulties in the computation of whole-stock fishing mortality rates. Fishing mortality (*n*-weighted) is typically computed as the number removed per unit time divided by the total population. If some part of the stock is fished less than average, then this subpopulation will be disproportionately overrepresented in the population as compared to the portion of recruits that came from this subpopulation. This causes a mismatch between the standard calculation of fishing mortality and per-recruit calculations because the estimated *n*-weighted fishing mortality will underestimate the mean fishing mortality when averaged over all recruits. This problem would be even more serious if biomass-weighted fishing mortalities were used.

To take a simple example, suppose a stock produces N_0 recruits annually and has a natural mortality rate of $M = 0.1$. Suppose 90% of the recruitment occurs in an area where the fishing mortality on recruited individuals $F_1 = 1.0$, independent of age. At equilibrium, this subpopulation will have $0.9N_0/(M + F_1)$ surviving members (Beverton and Holt 1957). The other 10% of the recruitment occurs in an area where the fishing mortality $F_2 = 0.1$, independent of age. This subpopulation will have $0.1N_0/(M + F_2)$ surviving members at equilibrium. Thus, the proportion of the stock from the first subpopulation is

$$(1) \qquad \frac{0.9/(M + F_1)}{(0.9/(M + F_1)) + (0.1/(M + F_2))} = 0.62$$

The *n*-weighted fishing mortality is therefore $0.62(F_1) + 0.38(F_2) = 0.66$. However, the mean fishing mortality when each recruit is given equal weight is much higher (0.91). Thus, $F = 0.66$ is not the mean (i.e., expected) fishing mortality of a recruit, nor would the yield obtained by a conventional YPR calculation with $F = 0.66$ represent the mean yield obtained from a recruit. In this simple example, it would be possible to resolve these difficulties by dividing the stock into two parts, and calculating the correct fishing mortalities and YPR for each part. However, in more complex situations, such subdivision of stocks may be neither practical nor desirable.

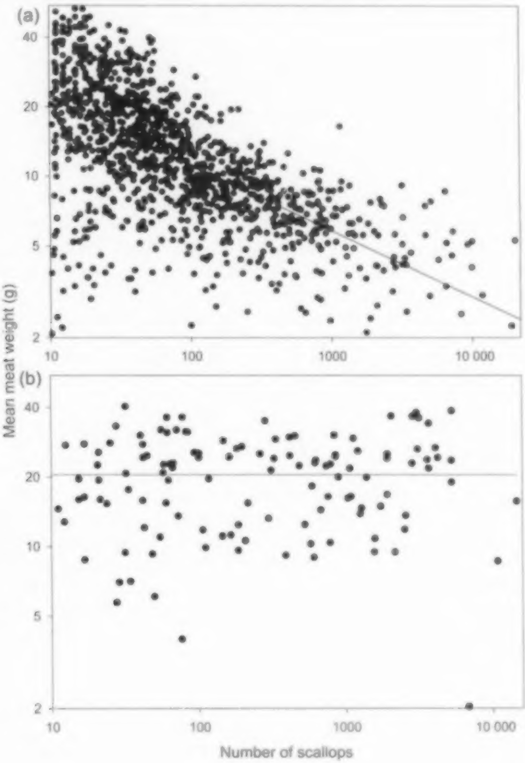
Variations in fishing mortality risk within a stock are likely to be common. Fishers attempt to maximize their profits by fishing in those areas where their net revenue per unit time is high, often leading to spatial variation in fishing mortality (Caddy 1975; Gillis et al. 1993; Holland and Sutinen 1999). In species where individuals do not readily move between heavily and lightly fished areas, the implicit assumption in per-recruit analysis that all individuals suffer similar levels of fishing mortality can be strongly violated.

A good example of this phenomenon can be seen in sea scallops, *Placopecten magellanicus*, on Georges Bank in the Northwest Atlantic. Annual scallop surveys of the U.S. portion of Georges Bank and surrounding areas have been made since 1982 (see Serchuk and Wigley 1986). The average sea scallop meat weight of each tow of this survey from 1982 to 1994 is plotted on the *y* axis in Fig. 2*a*, excluding tows where fewer than 10 scallops were caught. The *x* axis of this plot presents the number of scallops caught on the tow. A clear pattern is seen in which large scallops are often observed in areas of low density, whereas in areas of high density, the average scallop meat weight is much smaller, and is around the size at which scallops recruit to the fishery.

In December 1994, three large areas on or near Georges Bank were closed to trawling and scallop dredging (Murawski et al. 2000). Figure 2*b* is similar to Fig. 2*a*, except it shows tows from the closed areas in 1999 and 2000 (excluding the southern portion of closed area II, which was reopened to fishing in 1999), after these areas had been closed for a number of years. In contrast to Fig. 2*a*, no relationship is present in Fig. 2*b* between density and average size. This indicates that the strong trend of decreased average size in high-density areas seen in Fig. 2*a* was a result of fishing activity. Fishing effort tends to be concentrated in productive, high-density areas, thereby inducing higher fishing mortality there. Thus, scallops that settle in high-density areas are typically fished before they can grow to the sizes often seen in areas of low productivity or in areas closed to fishing.

It was already noted by Beverton and Holt (1957) that such spatial variation in fishing mortality can complicate the relationship between effort and fishing mortality, and between fishing mortality and yield, so that the use of standard fisheries theory in this situation may produce incorrect results. Caddy (1975) pointed out that this problem is especially severe for sedentary and sessile stocks, and standard per-recruit theory may misestimate the actual YPR. He used explicit spatial simulations to show that traditional models that use a dynamic pool assumption may misestimate the yield obtained from the sea-scallop fishery. Unfortunately, the ideas of this pioneering work have often not been incorporated into the management of sedentary stocks. Part of the problem is that ad hoc spatial simulations lack the simplicity of traditional fisheries models, and that they seem to depend on the exact assumptions about the spatial configuration of the resource in the model. Another spatially explicit YPR

Fig. 2. (*a*) Mean meat weight of sea scallops on the U.S. portion of Georges Bank on each tow of the annual NMFS sea scallop survey between 1982 and 1994, plotted as a function of the number caught in the tow (tows where fewer than 10 scallops were caught were excluded). The linear (log–log) best least-squares fit to this data is also shown. (*b*) A similar plot, but of the tows conducted in 1999–2000 of areas on Georges Bank that had been closed to fishing since December 1994.



model for shellfish stocks was introduced by Murawski and Fogarty (1984), who focused on the effect of localized density-dependent growth and mortality on YPR.

Models that take into account individual variations within a population have become increasingly common in recent years (e.g., Huston et al. 1988; DeAngelis and Gross 1992). Such "individual-based" models have often shown that variations in life history parameters among individuals have important effects on population dynamics.

The purpose of this article is to present a general method of taking into account variations among individuals in fishing mortality in the context of YPR analysis. This individual-based modelling approach requires only a general assumption about variation of fishing mortality in the population, and can give the same type of fishing mortality and biomass reference points as traditional per-recruit approaches.

Methods

If the growth rates, natural mortality (M), and fishing mortality (F) are known for an individual recruit, the expected YPR $Y(F)$ for that recruit can be calculated as in conventional per-recruit analysis (e.g., Beverton and Holt 1957; Gulland 1983; Quinn and Deriso 1999). Note that in the context of computing individual YPR, mortality must be interpreted as a risk (i.e., a probability per unit time) rather than that the usual interpretation as a rate, and individual YPR needs to be interpreted as an expected value.

Here, a length-based per-recruit model for sea scallops was used to calculate expected individual yields (NEFSC 2001), similar to the "generic per-recruit model" described in Quinn and Deriso (1999). von Bertalanffy growth coefficients for shell heights (lengths) were obtained from Serchuk et al. (1979). M was set at 0.1 (Merrill and Posgay 1964). Shell heights L were converted into meat weight (potential yield) W by a shell height to meat weight formula of the form

$$\ln(W) = a + b\ln(L) \tag{2}$$

The parameters a and b were selected as the best least-squares fit to shell height and meat weight data. For Georges Bank, $a = -11.6038$ and $b = 3.1221$, whereas for the Mid-Atlantic Bight, $a = -12.2484$ and $b = 3.2641$ (NEFSC 2001). YPR and biomass per recruit (BPR) for individual recruits were then calculated by the formulas

$$Y(F) = \int_{a_0}^{a_f} F\theta(t)W(t)S_F(t)\mathrm{d}t \tag{3}$$

$$B(F) = \int_{a_0}^{a_f} W(t)S_F(t)\mathrm{d}t \tag{4}$$

where a_0 is the age (in years) at which the scallop reaches 40-mm shell height, $a_f = a_0 + 30$, $W(t)$ is the meat weight at age t, $\theta(t)$ is the selectivity at age t, and $S_F(t)$ is the fraction of the 40-mm recruits that survive to age t. The integrals were calculated numerically with a time step of 0.01 years.

In this article, the individual variations in fishing mortality risks is the only type of variability considered. The variation in fishing mortality can be described by a cumulative distribution function (CDF) $C(F)$, which gives the probability that a randomly chosen recruit will have a (fully recruited) fishing mortality risk of less than F. The expected YPR, $\overline{Y}$, of a randomly chosen recruit is then given by

$$\overline{Y} = \int_0^\infty Y(F)\mathrm{d}C(F) \tag{5}$$

In the case where $C(F)$ is differentiable, and so has a probability density function $c(F) = C'(F)$, then eq. 5 becomes

$$\overline{Y} = \int_0^\infty Y(F)c(F)\mathrm{d}F \tag{6}$$

Individual-based BPR can be modeled similarly. If an individual experiences a fishing mortality risk F, the (expected) BPR $B(F)$ for this individual can be computed by conventional means. The expected BPR of a randomly chosen individual is

$$\overline{B} = \int_0^\infty B(F)\mathrm{d}C(F) \tag{7}$$

To apply this theory in practice, it is necessary to estimate the CDF $C(F)$. One estimation technique will be discussed here, using sea scallops as an example. Estimating $C(F)$ requires calculating fishing mortality on a relatively fine spatial scale. Techniques that estimate fishing mortality from year-to-year variations in age classes are impractical on these spatial scales owing to the high variability of survey data. Because these techniques are based on differences between surveys in adjacent years, they tend to amplify the already high measurement error present at small spatial scales (Conte and de Boor 1980). Instead, fishing mortality was inferred by using local size-structure information, employing the formula of Ssentongo and Larkin (1973). This formula calculates total mortality Z from a given size structure, assuming von Bertalanffy growth, with parameters L_∞ and K, constant mortality and recruitment, and a constant total mortality rate for lengths greater than some length l_c. Assuming a large sample size, this formula is (Gulland 1983)

$$(8) \qquad Z = \frac{K}{\bar{y} - y_c}$$

where $y_c = \ln(1 - l_c/L_\infty)$, and $\bar{y}$ is the mean value over all individuals whose lengths l are greater than l_c of

$$(9) \qquad y = \ln(1 - l/L_\infty)$$

In sea scallops, lengths are scallop shell heights, and knife-edge recruitment is assumed to occur at $l_c = 80$ mm. Fishing mortality F was obtained by the formula $F = Z - M$, with $M = 0.1$. The Ssentongo and Larkin formula is less sensitive to measurement error than those techniques that difference year-to-year survey values.

The assumption of constant recruitment in the Ssentongo and Larkin formula is of course not even approximately correct. A large year class will cause this formula to overestimate fishing mortality when it is first recruited to the fishery, and then underestimate it in later years as the year class matures. So while this formula may not accurately measure fishing mortality for a single year, it would be expected to be a reasonably reliable estimator of fishing mortality when averaged over many years.

To check this idea, I ran Monte Carlo simulations where F was fixed but recruitment was varied lognormally, with the mean, variance, and autocorrelation of the simulated recruitment matching that of the observed 1982–1999 U.S. Georges Bank sea scallop recruitment time series. The mean of the Ssentongo and Larkin estimates over 4000 years was within 10% of the correct fishing mortality F over a broad range of input fishing mortalities, and the mean estimate over all runs with various fishing mortalities matched the mean input fishing mortality to within 4%. This indicates that variable recruitment causes this formula to have at most a small bias. The Ssentongo and Larkin estimates were then blocked into 13-year time segments and averaged. The means of the blocks had a standard deviation that ranged between 0.05 at low fishing mortalities up to about 0.15 at high fishing mortalities, about one fourth that of the standard deviation of the unaveraged annual estimates of Z. Thus, while recruitment events may make the Ssentongo and Larkin method unreliable for a single year, it should give a reasonable estimate of temporally averaged fishing mortality in an area when these estimates are averaged over a number of years. This formula is also not sensitive to the exact value of l_c (provided it is large enough to insure full gear selectivity); changing l_c from 80 mm to 90 mm affected the estimated values of Z in the simulations by less than 1%.

Annual National Marine Fisheries Service (NMFS) surveys of sea scallops have been conducted in Georges Bank and in the Mid-Atlantic Bight for the last 20 years (see Serchuk and Wigley 1986 for a more full description). I focused on the years 1982–1994, during which time both survey design and management measures were stable. After 1994, many management changes were made including closed areas, effort controls, and gear restrictions. This period may therefore not be comparable to previous years, and was excluded from the analysis. The surveys were based on a random stratified design, with the surveyed area divided into a number of strata defined by depth and region.

Mean recruitment r_i (per tow) was calculated for each survey stratum i over the time period 1982–1994. Recruits were defined as those scallops between shell heights of 40 mm (the smallest size reliably detected in the survey) to those corresponding to an age one year older than a 40-mm scallop, as estimated by von Bertalanffy growth equations (69 mm in the Mid-Atlantic Bight and 72 mm in Georges Bank). If the area of stratum i is a_i, then the probability that a recruit chosen randomly over that time period was in that stratum is

$$(10) \qquad p_i = \frac{a_i r_i}{\sum_j a_j r_j}$$

where the summation is taken over all strata. Mean fishing mortality F_i was estimated in each stratum i over the 1982–1994 time period by calculating fishing mortality for each year by the Ssentongo and Larkin formula and then averaging over the years in the time period. The CDF $C_0(F)$, the probability that a randomly chosen recruit was subject to a fishing mortality less than F during that time period, can be estimated as

$$(11) \qquad C_0(F) = \sum_{\{i: F_i < F\}} p_i$$

This gives an estimate of the historic CDF, based on past fishing patterns. To perform per-recruit analysis, it is necessary to compute the YPR for a variety of (mean) fishing mortalities, not just the one observed historically. Here, I will make the simple assumption that changing the mean fishing mortality does not affect the variability in that mortality. In other words, if F_h represents the mean (recruit-weighted) historical fishing mortality, then the CDF $C_1(F)$ for a different mean fishing mortality F_1 is given by

$$(12) \qquad C_1(F) = C_0\left(\frac{F_h}{F_1} F\right)$$

The above procedure for estimating the fishing mortality CDF neglects within-stratum and year-to-year variation in fishing mortality, and is thus likely to somewhat underestimate the true individual variability in fishing mortality. Further uncertainty may be introduced by the estimation of the fishing mortality CDFs. However, the method described above is still a reasonable first approximation, and is useful in demonstrating the error made when variability in fishing mortality is neglected.

Results

To explore the effect on YPR of variation of fishing mortality, YPR curves were computed (Fig. 3) from eq. 5 using a uniform probability distribution in which fishing mortality levels range by 0%, 25%, 50%, and 100% about the recruit-weighted mean fishing mortality F_0 (i.e., fishing mortalities are distributed uniformly on the interval $((1 - a)F_0, (1 + a)F_0)$, where $a = 0, 0.25, 0.5, 1$, respectively). The x axis in Figs. 3a–3c represent recruit-weighted, number-weighted, and biomass-weighted fishing mortalities, respectively.

In all cases, individual deviations in fishing mortality risk tends to reduce YPR when the mean fishing mortality is near $F_{\max}$, especially when variability is high. When recruit-weighted fishing mortalities are employed, variability in fishing mortality induces an increase in YPR at high fishing mortality rates. However, if biomass-weighted fishing mortalities are used, this variability causes considerable reductions in YPR at high fishing mortality rates. Results with number-weighted fishing mortalities fall between those employing recruit-weighted and biomass-weighted fishing mortalities.

Individual-based BPR curves are given in Fig. 4. Variation in fishing mortality causes the standard theory to underestimate actual recruit-weighted BPR. This is especially apparent at intermediate fishing mortality levels, where the

Fig. 3. Individual-based yield-per-recruit (YPR) curves assuming fishing mortality varied uniformly in the interval $((1 - a)F_0, (1 + a)F_0)$, where $a = 0$ (solid line), 0.25 (dotted line), 0.5 (broken line), and 1 (broken dotted line). In part (*a*), the *x* axis represents recruit-weighted fishing mortality F_0, whereas in (*b*) and (*c*), the *x* axis is number-weighted and biomass-weighted fishing mortalities, respectively.

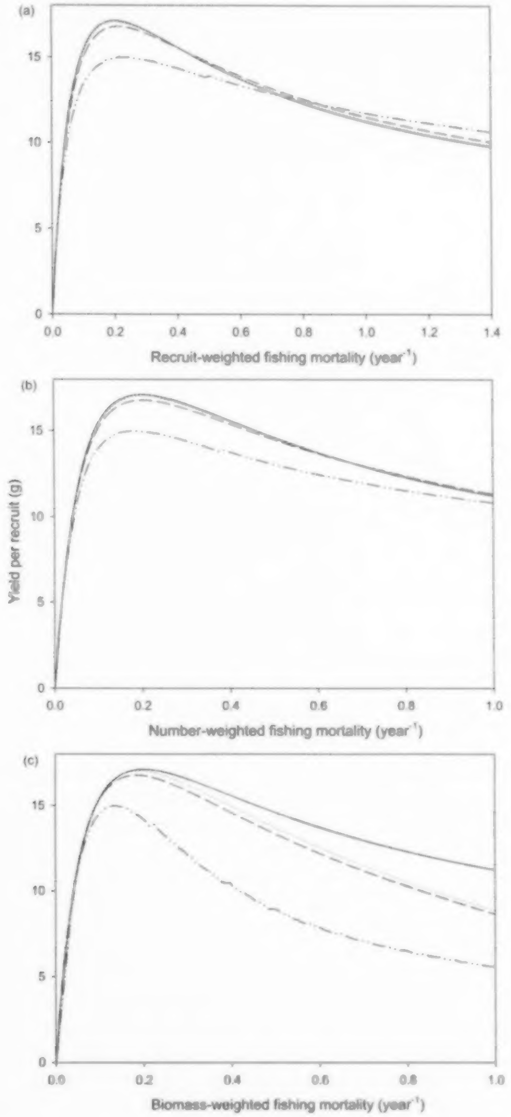
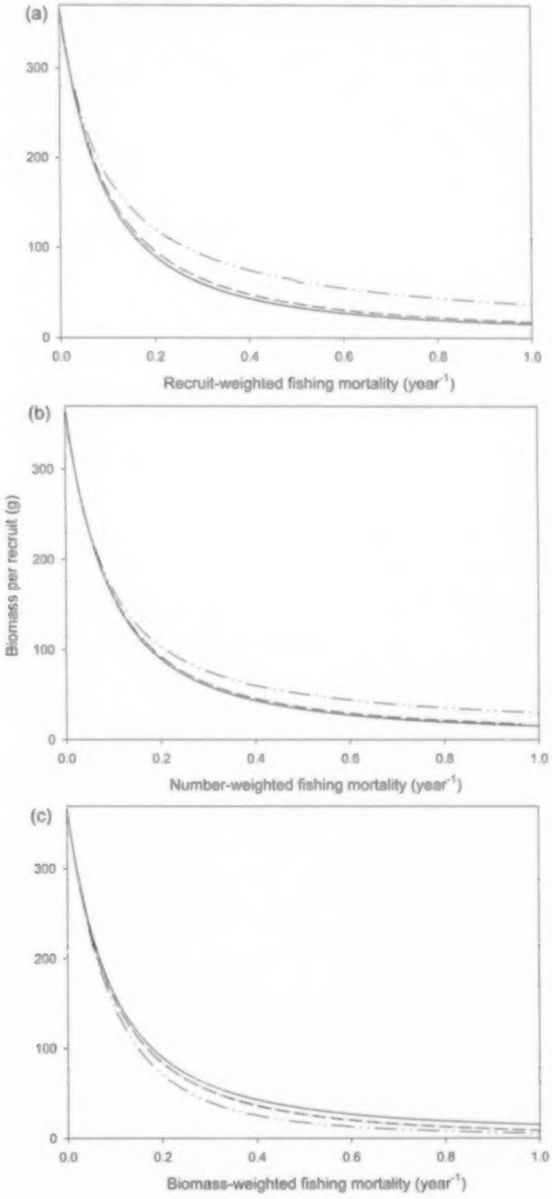


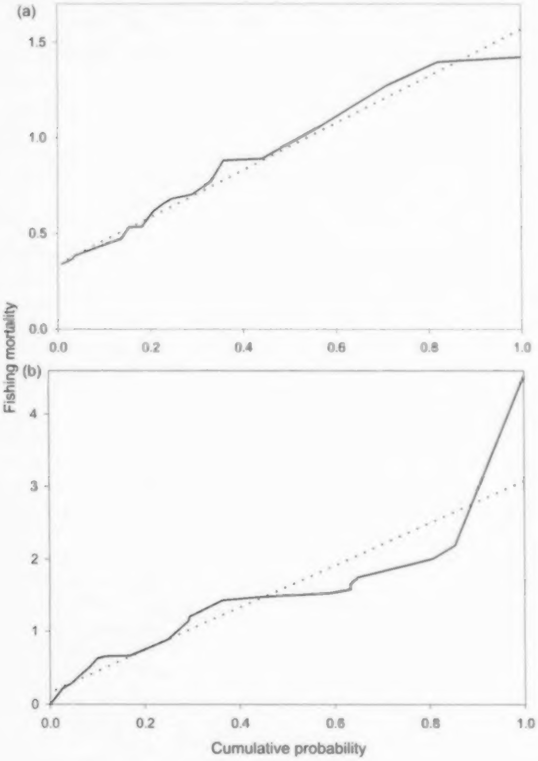
Fig. 4. Individual-based biomass-per-recruit (BPR) curves assuming fishing mortality varied uniformly in the interval $((1 - a)F_0, (1 + a)F_0)$, where $a = 0$ (solid line), 0.25 (dotted line), 0.5 (broken line), and 1 (broken dotted line). In part (*a*), the *x* axis represents recruit-weighted fishing mortality F_0, whereas in (*b*) and (*c*), the *x* axis is number-weighted and biomass-weighted fishing mortalities, respectively.



nonlinearity of the conventional BPR curve is the greatest. A similar, though quantitatively weaker, pattern is seen when fishing mortality is number weighted. For biomass-weighted mortality, individual variation causes a decreased BPR at a given fishing mortality.

Cumulative probability distributions were estimated for the U.S. portion of Georges Bank and for the Mid-Atlantic Bight over the years 1982–1994 (Fig. 5). Both CDFs show high spatial variability in fishing mortality, with the highest fishing mortality located in the most productive areas of the two regions (the Great South Channel area of Georges Bank, and the Hudson Canyon area in the Mid-Atlantic Bight). Variability appears to be higher in the Mid-Atlantic Bight than in Georges Bank. In both cases, the estimated CDFs are

Fig. 5. Estimated cumulative distribution functions of sea-scallop fishing mortality during the years 1982–1994 for (*a*) the U.S. portion of Georges Bank, and (*b*) the Mid-Atlantic Bight.



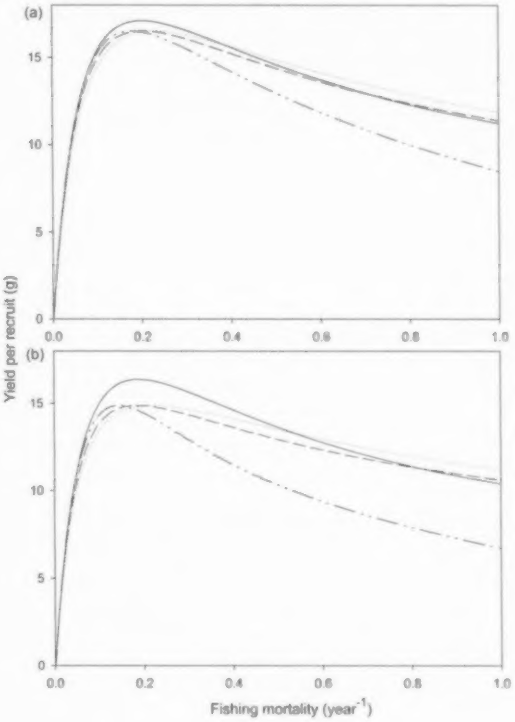
approximately linear; the slight nonlinearities are most likely artifacts of the coarse nature of the survey design. Thus, it is reasonable to approximate both of these empirical CDFs with their best least-squares fitted lines, corresponding to uniform probability distributions.

Individual-based YPR and BPR curves for these two regions are given in Figs. 6 and 7. The higher variability in fishing mortality in the Mid-Atlantic Bight induced a larger deviation from the conventional per-recruit curves in this region than in Georges Bank.

Discussion

The analysis performed here indicates that variation in fishing mortality risk among recruits (caused by, for example, spatial variation in fishing mortality) can alter the YPR and BPR that would be predicted by conventional theory. For a typical YPR curve that contains a single inflection point, standard theory will overestimate yield at low fishing mortalities where the YPR curve is concave, and underestimate it at high fishing mortalities where it is convex, when fishing mortalities are recruit-weighted. This is the "Jensen's inequality effect" discussed in the Introduction. Note that the conventional and individual-based YPR curves do not necessarily cross exactly at the point of inflection. Jensen's inequality gives no information in the case where the fishing mortality of some recruits are on each side of the inflection point. Thus, the two lines can cross at any point in a broad range of values near the point of inflection.

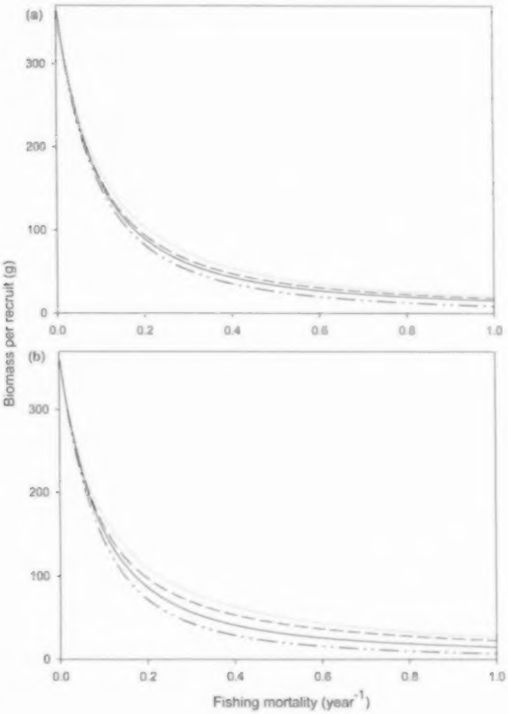
Fig. 6. Calculated individual-based yield-per-recruit (YPR) for (*a*) the U.S. portion of Georges Bank, and (*b*) the Mid-Atlantic Bight. For each curve, YPR plots were created with three different methods of estimating mean fishing mortality on the *x* axis: recruit-weighted *F* (dotted line), number-weighted *F* (broken line), and biomass-weighted *F* (broken dotted line). The solid line indicates the corresponding standard YPR curve.



More radical departures from the conventional YPR curve are seen when fishing mortality is weighted by number or biomass. As discussed in the introduction, number- and biomass-weighted fishing mortalities tend to overweight the fishing mortality of those recruits whose fishing mortality risk is below average, because these individuals will be overrepresented in the population. The relatively low fishing mortality on this portion of the population masks the high fishing mortality on the other part of the population. This phenomenon is especially apparent when there is high variability in fishing mortality and (or) high mean fishing intensity. The net effect is to lower the number- and biomass-weighted $F_{\max}$, and lower the predicted yield for fishing mortalities above $F_{\max}$ compared with its value when using recruit-weighted fishing mortalities.

Because BPR curves are typically convex, Jensen's inequality implies that individual variation in fishing mortality would increase BPR compared with conventional theory. Intuitively, the increase in BPR from those individuals whose fishing mortality is below the recruit-weighted average is greater than the loss in BPR from those individuals whose fishing mortality is greater than average, thus inducing a net

Fig. 7. Calculated individual-based biomass-per-recruit (BPR) analysis for (*a*) the U.S. portion of Georges Bank and (*b*) the Mid-Atlantic Bight. For each curve, BPR plots were created with three different methods of estimating mean fishing mortality on the *x* axis: recruit-weighted *F* (dotted line), number-weighted *F* (broken line), and biomass-weighted *F* (broken dotted line). The solid line indicates the corresponding standard BPR curve.



increase in BPR. This pattern is reversed when biomass-weighted fishing mortality is employed, because the mean biomass-weighted fishing mortality is considerably smaller than the corresponding recruit-weighted fishing mortality, thereby inducing a lower BPR at a given fishing mortality.

Analysis of the U.S. Georges Bank and Mid-Atlantic Bight sea scallop data demonstrates that there was indeed high spatial variability in fishing mortality in these stocks. At the fishing mortalities typical of the 1982–1994 period ($F = 1$, *n*-weighted), the results indicate that standard theory would have mildly underestimated both BPR and YPR using number-weighted fishing mortalities. However, the use of biomass-weighted fishing mortalities would have induced the conventional theory to considerably overestimate YPR and BPR. This suggests that, when applying per-recruit theory, it is not advisable to employ biomass-weighted fishing mortalities. At more optimal levels of fishing mortality, these YPR curves indicate that spatial variation in fishing mortalities may induce a greater than 10% loss in YPR.

Motivated by simplicity and the form of the estimated sea scallop CDFs, the analyses conducted here assumed linear fishing mortality CDFs. However, in some cases, the variations in fishing mortality may be more extreme than that implied by uniform distributions, leading to a nonlinear CDF. In such a case, actual YPR and BPR may deviate from those predicted by conventional theory even more strongly than was found here.

The formula of Ssentongo and Larkin has been criticized on the grounds that it is very sensitive to observed lengths near L_∞ (Powell 1979; Hoenig et al. 1983). This was not an issue in the present study because high mortality rates kept most of the population lengths well below L_∞. In cases where there are substantial numbers of individuals near L_∞, alternative estimators of mortality, such as those derived by Beverton and Holt (1956) or Powell (1979), should be used. To check the robustness of Ssentongo and Larkin formula in the present case, I compared these estimates of mortality to that obtained by the Beverton and Holt estimator. Time-averaged mortality for survey strata obtained from the Beverton and Holt formula deviated on average from that of Ssentongo and Larkin by less than 8%, and the overall mean fishing mortalities for the two methods were within 2% of each other. Thus, the mortality estimates in the present study do not appear to be strongly sensitive to the form of the mortality estimator that is employed. Further discussion of relative merits of various methods of estimating mortality rates from length-frequency data can be found in Wetherall et al. (1987).

A strong correlation was observed between productivity (as measured by mean recruitment) and fishing mortality, indicating that fishers were generally concentrating on those areas where catch rates were the highest. Differences in fishing costs among regions can also lead to spatial variations in fishing mortality, with higher fishing mortalities in the lower-cost areas. Such behaviour can be more economically efficient than spatially uniform fishing. A "utility-per-recruit" analysis that calculates, e.g., net revenue per recruit, may be of more interest to managers and fishers in this case than YPR analysis (Die et al. 1988). If costs and prices are known as a function of space and size, it would be straightforward to extend the theory presented here to compute individual-based utility per recruit.

While the emphasis here is on broad spatial variation in fishing mortality, the theory developed can be applied to any situation where fishing mortality risk varies among recruits. For example, recruits that were born at different times of the year might experience different fishing mortality risks. Local refugia could lower the fishing mortality risk for some recruits, again inducing individual variation in that quantity. Even in more mobile species, phenomena such as spawning aggregations may induce variations in fishing mortality risk within the stock.

Similar techniques could also be applied to analyze the effects of individual variations in growth and (or) natural mortality. However, the effects of variability of these factors on YPR are likely to be smaller than those stemming from individual differences in fishing mortality, because the nonlinearity in the relationship between YPR and BPR and fishing mortality is much stronger than that of growth or natural mortality.

If the fishery management system lacks any spatial controls on fishing of sedentary stocks, my results indicate that at fishing mortalities near $F_{\max}$, a reduction in yield compared to spatially uniform fishing will likely occur owing to the concomitant variations in fishing mortality among recruits. Further losses may occur if a number- or biomass-weighted fishing mortality metric is improperly matched with a standard YPR $F_{\max}$ target, thereby causing the stock to be subtly overfished.

Some type of area management is therefore necessary in sedentary stocks to maximize yield. One possibility is to manage high- and low-productivity regions separately, as is currently being done in the Canadian sea-scallop fisheries. A second possibility is an area rotation system. Temporarily closing areas with high densities of small animals can help reduce the loss of yield that would occur from localized overfishing of these areas. Rotational systems have been successfully implemented for a number of sedentary invertebrate stocks, and are currently under consideration for the U.S. Atlantic sea scallop fishery.

Even if area management is not practical, managers should at least employ a recruit-weighted fishing mortality metric that matches more closely the standard YPR theory. Alternatively, if it is desired to retain number- or biomass-weighted fishing mortality metrics, reference points need to be set to the corresponding individual-based number- or biomass-weighted maximal YPR, rather than the standard YPR reference points.

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Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy)

David B. Arscott, Klement Tockner, and J.V. Ward

Abstract: Daily and seasonal water temperature patterns were investigated at 22 habitats in five geomorphic reaches along an Alpine-Mediterranean river. Study reaches spanned 2nd- to 7th-order river segments. Habitats included headwater streams, main and secondary channels, backwaters, and isolated pools. Multiple linear regression analyses extracted elevation and azimuth (aspect) out of eight geographical and environmental variables to explain average daily temperature patterns among habitats. Azimuth and, to a lesser degree, slope, depth, velocity, and canopy were primary determinants of diel temperature amplitude and maximum rates of diel heating and cooling. Within lowland floodplain reaches, the relative influence of groundwater and surface water varied substantially among habitats. Thermal variation among habitats was greatest in lowland floodplain reaches (nearly 15°C difference). In summer and autumn, variation between lowland floodplain aquatic habitats exceeded thermal variation observed in the main channel along the entire river corridor (120 km; 5–1100 m above sea level). Spatiotemporal variation in temperature was greatest in lower reaches owing to the interaction of water level and connectivity of isolated water bodies. Influence of groundwater and cool-water tributaries exemplified the importance of local factors (geomorphology and hydrology) superimposed on regional factors (climate and altitude) in determining large-scale thermal patterns.

Résumé : Les patterns journaliers et saisonniers de la température de l'eau ont été étudiés dans 22 habitats appartenant à 5 sections géomorphologiques le long du cours d'une rivière méditerranéenne alpestre. L'étude couvrait des segments de rivière d'ordres 2 à 7. Les habitats comprenaient des ruisseaux d'amont, des cours principaux et secondaires, des eaux dormantes et des profonds isolés. Une analyse de régression multiple linéaire a identifié, comme les meilleures variables explicatives des patterns de température dans les habitats, l'altitude et l'azimut (l'exposition) parmi huit variables géographiques et environnementales. L'azimut, et à un degré moindre, la pente, la profondeur, la vitesse du courant et la couverture végétale étaient les facteurs déterminants de l'amplitude journalière de la température et des taux maximaux de réchauffement et de refroidissement journaliers. Dans les tronçons de la plaine d'inondation, l'importances relative des eaux souterraines et des eaux de surface variait considérablement d'un habitat à l'autre. La variation thermique entre les habitats était maximale dans les secteurs de terres basses de la plaine d'inondation (une différence de près de 15°C). En été et en automne, la variation thermique entre les habitats aquatiques des terres basses de la plaine d'inondation dépassait la variation observée dans le cours principal dans tout le couloir de la rivière (120 km; 5–1100 m au-dessus du niveau de la mer). La variation spatio-temporelle de la température était maximale dans les tronçons les plus bas à cause de l'interaction entre le niveau de l'eau et la connectivité des masses d'eau isolées. L'influence des eaux souterraines et des tributaires à eaux fraîches illustre l'importance des facteurs locaux (la géomorphologie et l'hydrologie) qui se superposent aux facteurs régionaux (le climat et l'altitude) pour établir les patterns de température à grande échelle.

[Traduit par la Rédaction]

Introduction

Temperature has been repeatedly recognized as a key environmental variable structuring both aquatic invertebrate (e.g., Vannote and Sweeney 1980; Ward and Stanford 1982; Hawkins et al. 1997) and fish (e.g., Illies 1961; Welcomme 1979; Torgersen et al. 1999) communities. Kinne (1963) suggested that "…temperature is presumably the most important single environmental entity" and Kamler (1965) stated that temperature is a major factor controlling distribution of aquatic insects, with the degree of thermal fluctuation being the most important aspect of the thermal pattern.

The river zonation scheme developed by Illies (1961) and Illies and Botosaneau (1963) demonstrated that downstream changes in water temperature corresponded to transitions in zoobenthic and fish communities. The River Continuum

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Concept (RCC; Vannote et al. 1980) described lotic systems as resource gradients from the headwaters to the sea and hypothesized predictable downstream changes in temperature regime. In particular, RCC (and the study of Vannote and Sweeney 1980) presented evidence that the maximum daily temperature pulse is greatest in 4th- or 5th-order river segments. Temperature pulses were predicted to be lower in smaller headwaters owing to shading by riparian vegetation and close proximity to source waters and lower in larger river reaches because the greater volume of water creates a greater thermal buffering capacity. They further hypothesized that biotic communities were predictably structured along the longitudinal continuum, with species diversity maximized in mid-order reaches where thermal heterogeneity is greatest.

Physical factors influencing water temperature are numerous and interrelated (Poole and Berman 2001). Hydrological variables influencing temperature include the source of the water, relative contribution from groundwater, current velocity (a function of channel form, water volume, and substrate type), and discharge (Smith 1972). Latitude, altitude, and continentality represent regional-scale physical variables that influence water temperature (Ward 1985). Local-scale physical variables include channel form and orientation, vegetation cover, and type of bottom substrate (Hawkins et al. 1997). Climatic factors include air temperature, vapor pressure, wind speed, and precipitation. For thorough reviews of the mechanistic influence of these factors on stream temperatures refer to Smith (1972) and Ward (1985).

Current understanding of the ecological responses to temperature (e.g., Vannote and Sweeney 1980; Ward and Stanford 1982; Hawkins et al. 1997) and temperature patterns in riverine environments (e.g., Smith and Lavis 1975; Evans and Petts 1997; Constantz 1998) has been derived primarily from studies of single-channel river systems or from the main channel of multichannel systems. Consideration of the physical complexity or ecological implications of thermal patterns in flood plains or multichannel systems has been limited to only a few studies (e.g., Mosley 1983; Tockner et al. 2000; Malard et al. 2001). Moreover, much of the literature published on stream temperature has described changes in thermal regimes owing to human impacts (e.g., forestry practices or urbanization), leaving a paucity of information on natural dynamics and heterogeneity of thermal patterns in unimpacted running waters, particularly complex alluvial flood plains. In natural river flood plains, a gradient of water-body types exists across the riverine landscape (flowing channels to standing water bodies), which is a function of local geomorphological characteristics and hydrological interactions. Environmental conditions in floodplain water bodies respond to water-level fluctuations (Junk et al. 1989), often resulting in marked changes in water quality, shear forces (i.e., from lentic to lotic or vice versa), and, most likely, thermal conditions.

The aim of this study was to quantify aquatic thermal patterns along a floodplain river (Tagliamento River, Italy) and to determine the extent to which prevailing concepts of thermal variation along the river continuum were applicable to this river system. Describing thermal patterns requires a multiple scale and multiple factor approach that includes seasonal and diel patterns as well as factors such as annual and monthly degree-days and daily rates of temperature heating and cooling. Specifically, we were interested in (*i*) determining downstream changes in thermal patterns and variation, (*ii*) illustrating how thermal patterns in different habitats (i.e., side channels, backwaters, and pools) contribute to thermal heterogeneity in river ecosystems, and (*iii*) determining which geographic and environmental factors were associated with variation in different thermal variables. We had two primary hypotheses: first, that across a single flood plain, lateral thermal heterogeneity between various aquatic habitats can be greater than longitudinal thermal variation along the main channel of an entire river; and second, that local geomorphological characteristics determine the degree to which hydrology controls temperature change in floodplain channels and lateral aquatic habitats.

Materials and methods

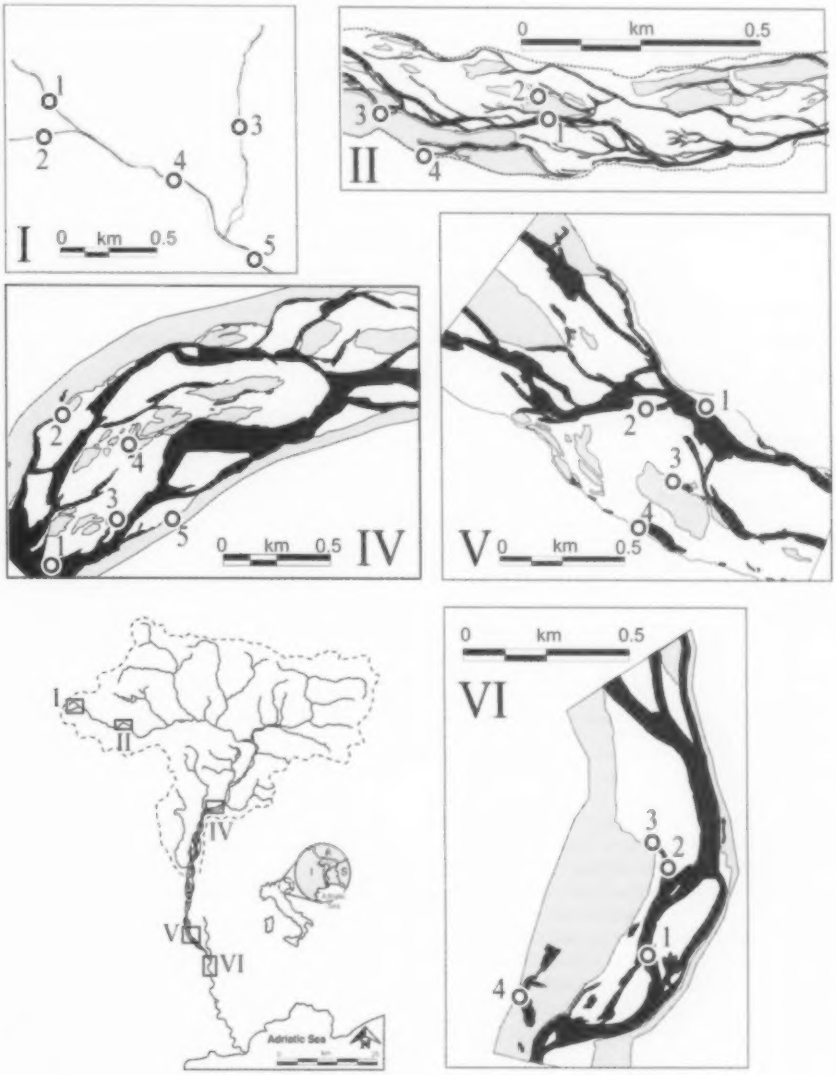
Study site

The Tagliamento catchment, located in northeastern Italy, borders Austria to the north and Slovenia to the east (Fig. 1). The mainstem corridor is approximately 172 km long and flows from headwaters in the limestone–dolomite Alps (maximum elevation 2700 m above sea level (asl)) to the Adriatic Sea midway between Venice and Trieste where it empties as a 7th-order river. The hydrological character of the Tagliamento mainstem is described as a flashy pluvionival regime, with highest discharges during the spring and autumn (see Results for further description of the hydrology). Glaciofluvial sediments (size range 2–64 cm) dominate, and the aquatic substratum consists of a complex mixture of silt, sand, gravel, cobble, and boulders (Arscott et al. 2000; Petts et al. 2000). In some locations along the river corridor, the glaciofluvial sediments are so porous and the alluvium so deep that the river's entire surface flow infiltrates the sediments under low-flow conditions (Ward et al. 1999), a natural feature of many Mediterranean rivers (Gasith and Resh 1999).

Geomorphic structure of a river section influences the processes that occur along the main channel and in laterally configured water bodies. For example, hydraulic conductivity (a measure of sediment permeability), surface morphology, and subsurface aquifer structure interact to control the degree to which a water body is connected with phreatic and hyporheic waters (Wondzell and Swanson 1996, 1999; Poole 2000). This connectivity has important implications for water temperatures and thermal buffering capacity of individual water bodies (Poole and Berman 2001). To investigate thermal heterogeneity, we selected five discrete reaches along the Tagliamento representing different geomorphological styles (Fig. 1). These reaches were classified as constrained headwater streams (1005–1200 m asl), a headwater island-braided flood plain (705 m asl), a lower island-braided flood plain (180 m asl), a braided-to-meandering transitional flood plain (10 m asl), and a meandering flood plain (5 m asl). We designated these reaches with Roman numerals I to VI in a previous study (Arscott et al. 2000) and, for consistency, retain the same notation (no data are presented for reach III).

Within each reach, we identified several specific habitat types (e.g., main channel, alluvial channel, backwater). Water flowing into each habitat was derived primarily from surface water, groundwater, or a combination of the two. The relative importance of surface water or groundwater varied among habitat types and with the flow pulse. Therefore, we measured and compared temperature dynamics in available habitat types within each geomorphic reach. Twenty-two study habitats were located throughout the five geomorphic reaches described above and were selected to encompass the range of aquatic habitats associated with the lateral configuration of a given reach (Fig. 1). Five headwater streams

Fig. 1. The location of the five study reaches (Roman numerals) in the Tagliamento catchment, northeast Italy, and each study habitat within those reaches (Arabic numerals). Light gray represents vegetated areas, black represents water, and white represents areas of open gravel (all reaches are surrounded by vegetated riparian zones).



including three separate 2nd-order tributaries and two downstream segments (i.e., a 3rd- and 4th-order segment) represented the constrained headwater streams (reach I). All habitats are described in Table 1 and Fig. 1.

Data collection

Water temperature was recorded hourly from each water body by installing VEMCO Minilog (TR model, VEMCO Limited, Shad Bay, N.S., Canada) temperature data loggers (–5 to 35°C, ±0.2°C). Before deployment, each data logger was placed in a temperature-controlled water bath to test the working range and to assess the accuracy of measurement. Differences between temperature loggers and water bath temperature averaged 0.1°C with maximum deviations of 0.2°C. Therefore, no correction factor was applied to the data derived from the loggers. Each data logger was placed into a protective stainless steel casing (~2.5 kg), fixed with a rope to the nearest tree or stable feature, and placed on the bottom of the water body. The casings were tested for effects on temperature measurement (Malard et al. 2001) and found to be of minimal influence to instantaneous temperatures (±0.1°C). Temperature loggers were deployed in all water bodies from 8 May 1998 to 25 June 1999. Loggers were placed in the deepest part of lentic water bodies and in flowing-water areas of lotic channels.

Air temperature, precipitation, and river stage height were acquired from local authorities (Presidenza del Consiglio dei Ministri, Ufficio Idrografico e Mareografico di Venezia, Sezione di Udine). Air temperature and precipitation were obtained from five locations that encompassed the entire range of elevation studied (2–1298 m asl). Stage height was obtained from a location at river-km 84 (immediately downstream of reach IV at 130 m asl) where the river was 7th order.

Elevation above sea level, floodplain slope, and floodplain azimuth were measured from 1:10 000 topographic maps (Regione Autonoma Friuli). Slope was verified in the field using a clinome-

Table 1. Geomorphic and environmental variables determined for each study habitat along the Tagliamento River.

Geomorphic unit or habitat description	Elevation (m asl)	Azimuth (degrees)	Slope (%)	Width (m)	Area (m^2)	Z_{max} (cm)	Discharge ($L \cdot s^{-1}$)	Current velocity ($m \cdot s^{-1}$)	Canopy (%)
I. Constrained headwater streams									
1. 2nd order	**1070**	**35**	**5.5**	**1.5**	—	**40**	**70**	**0.50**	**90**
2. 2nd order	1095	–90	19.5	2	—	30	64	0.38	0
3. 2nd order	1080	10	11	3	—	60	186	0.59	90
4. 3rd order	**1040**	**–50**	**5.5**	**2.5**	—	**40**	**222**	**0.36**	**100**
5. 4th order	**1005**	**–50**	**5.5**	**6**	—	**80**	**434**	**0.94**	**45**
II. Headwater island-braided flood plain									
1. 4th-order main channel	**705**	**–80**	**2.5**	**14**	—	**120**	**1 900**	**0.89**	**0**
2. Alluvial channel	705	–80	2.5	7	—	70	135	0.30	0
3. Alluvial channel	705	–80	2.5	5	—	25	13	0.20	10
4. Alluvial channel	705	–80	2.5	2	—	40	14	0.29	85
IV. Lower island-braided flood plain									
1. 7th-order main channel	**180**	**60**	**1**	**80**	—	**150**	**23 000**	**1.38**	**0**
2. Side channel	180	60	1	10	—	100	nd	0.24	50
3. Backwater	180	60	1	15	11 550	100	—	0.00	0
4. Pool near main channel	180	60	1	7	110	75	—	0.00	0
5. Pool far from main channel	180	60	1	6	100	40	—	0.00	40
V. Braided-to-meandering transition flood plain									
1. 7th-order main channel	**10**	**–40**	**0.5**	**90**	—	**140**	**2 500**	**0.45**	**0**
2. Backwater	10	–40	0.5	14	1 008	150	—	0.00	0
3. Pool near main channel	10	–40	0.5	12	920	140	—	0.00	25
4. Pool far from main channel	10	–40	0.5	40	6 429	120	—	0.00	5
VI. Meandering flood plain									
1. 7th-order main channel	**5**	**–9**	**<0.5**	**70**	—	**180**	**13 000**	**0.86**	**0**
2. Backwater	5	–9	<0.5	13	1 139	120	—	0.00	5
3. Pool near main channel	5	–9	<0.5	6	96	75	—	0.00	10
4. Pool far from main channel	5	–9	<0.5	37.5	6 066	120	—	0.00	90

Note: Bolded values indicate main channel habitats; all others are lateral water bodies. See Fig. 1 for habitat locations. m asl = metres above sea level. Width, area, Z_{max} (depth), discharge, and current velocity were measured at times of average flow conditions and therefore are only approximations of relative sizes and relative flow volumes. nd = no data.

ter. Azimuth was measured as the clockwise angle (in degrees) that the longitudinal orientation of the flood plain differed from due south (i.e., due west = 90°, due east = –90°; Hawkins et al. 1997). Channel width or maximum habitat width (for isolated water bodies and backwaters) was measured from digitized maps created in the field using a differential global positioning system (DGPS) accurate up to 0.3 m (D.B. Arscott, unpublished data). Maximum depth was measured directly in the vicinity of the temperature data logger. Percent canopy was estimated in the field for the area adjacent to the temperature data logger (ca. 10 m radius), current velocity was measured at four points across a transect using a MiniAir 2 meter (Schiltknecht Messtechnik AG, Gossau, Switzerland) during base-flow conditions, and specific conductance (T_{ref} = 20°C) was measured once a month for 12 months with a WTW LF320 conductivity meter (WTW Gmbh, Weilheim, Germany).

Data analysis

We used three statistical approaches to investigate thermodynamics along longitudinal and lateral gradients. First, multiple linear regression analysis was used to extract explanatory variables (geographic and environmental) for patterns observed among the 22 habitats. Second, thermal degree-days (annual and monthly) were calculated to determine the influence of thermal energy available to aquatic organisms. Thermal degree-days represent an integrated measure of thermal summation over monthly and annual time scales and offer another perspective, which summarizes spatial and temporal variability in the thermal environment using a comparative approach. Finally, PCA (principal components analysis) was used to summarize spatial patterns (longitudinal and lateral) of several thermal variables calculated for all habitats.

Multiple linear regression analysis

Forward stepwise multiple regression analyses were used to determine geographic and environmental factors that were most strongly associated with variation in thermal variables among aquatic habitats in each of two seasons (summer and winter). The selection of two 3-week periods, one in summer and one in winter, was based on two primary criteria: first, having data from the warmest and coolest parts of the year; and second, periods needed to coincide with parts of our thermal records that contained the fewest missing data points.

We were primarily interested in determining the influence of environmental factors on three types of thermal data: (*i*) absolute temperature, (*ii*) diel patterns in temperature, and (*iii*) relative rates of daily temperature change. Initially, eight thermal (dependent) variables representing these groups were calculated and these included (*i*) average daily mean temperature, (*ii*) average minimum daily temperature, (*iii*) average maximum daily temperature, (*iv*) average diel temperature pulse, (*v*) maximum diel temperature pulse, (*vi*) average of Kamler's coefficient of daily thermal astatism (Kamler 1965), (*vii*) maximum rate of thermal heating, and (*viii*) maximum rate of thermal cooling. Kamler's coefficient was calculated as the daily maximum temperature divided by daily minimum temperature. Formulas for computation of daily average temperature, daily temperature pulse, and maximum rate of thermal heating and cooling are reported in Table 2. For the multiple

Table 2. Four thermal variables[a] used in statistical analysis and their formulas.

Daily average temperature	$\bar{T}_{\mathrm{d}} = \frac{\sum_{i=1}^{n} X_i}{n}$	(1)
Daily temperature pulse	$\mathrm{TP_d} = T_{\max} - T_{\min}$	(2)
Maximum rate of thermal increase[b]	$\mathrm{TI}_{\max} = \frac{\sum X_i Y_i - \frac{(\sum X_i)(\sum Y_i)}{n}}{\sum X_i^2 - \frac{(\sum X_i)^2}{n}}$	(3)
Maximum rate of thermal cooling[b]	$\mathrm{TC}_{\max} = \frac{\sum X_i Y_i - \frac{(\sum X_i)(\sum Y_i)}{n}}{\sum X_i^2 - \frac{(\sum X_i)^2}{n}}$	(4)

Note: X_i, temperature at each time (5 min) interval i; Y_i, time at each measurement of X at i; n, total number of measurements during the 24-h period (288).

[a] Each variable was calculated for summer (8–28 July 1998) and winter (1–21 December 1998) time series consisting of continuous hourly measurements occurring from 0000 to 2355.

[b] Maximum rate of thermal increase and cooling were calculated by computing the slope of the linear regression (eqs. 3 and 4) through three measurements (previous hour, current hour, and future hour), thus creating 24 measures of heating or cooling rates per day. The maximum value was selected for $\mathrm{TI}_{\max}$ and the minimum was selected for $\mathrm{TC}_{\max}$.

regression analysis, thermal variables were computed as averages over the entire 3-week period (except where maximum or minimum was specified), and therefore, one value for each thermal variable represented summer or winter conditions. Dependent variables were regressed against eight geographical and environmental variables that included elevation, azimuth, floodplain slope, habitat width, maximum water depth, average current velocity, % canopy, and specific conductance. Because several of the thermal variables were suspected to be intercorrelated, Pearson's product moment correlation analysis was used to determine these relationships.

Thermal degree-days

Degree-days were calculated for habitats in which a full annual thermograph was successfully recorded or where missing data could be adequately modeled (see below). Degree-days were calculated by summing daily mean temperatures above 0°C, both monthly and for 1 year. Many thermal recordings were not continuous over the entire year owing to the loss of some data loggers as a result of floods and vandalism. Missing thermograph records from flowing-water habitats were replaced by predicted values based on model output from a nonlinear regression model reported by Mohseni et al. (1998). The regression model uses average weekly air temperatures to predict weekly average stream temperatures. We applied this formula to predict daily average stream temperatures based on daily average air temperatures recorded at a station midway along the Tagliamento mainstem (220 m asl at ca. river-km 60) and the partial records of daily average water temperature. Mohseni et al. (1998) found no significant effect of distance on the goodness of fit of the regression, even when using air temperatures from weather stations up to 244 km from the study stream. Warming data (later winter through midsummer) required separate regressions from cooling data (midsummer through midwinter) to account for seasonal hysteresis. Existing data were first fit to the model eq. 1 using the nonlinear regression analysis provided in Sigma Plot 2000 (SPSS Inc., Chicago, Ill.), which uses the Marquardt–Levenberg algorithm. If the regression met a priori criteria (significance at $p \leq 0.05$ and $R^2 \geq 0.70$), then the parameters were used to determine missing average daily temperatures from the respective stream-channel thermograph. Data created in this way were only used to calculate thermal degree-days for flowing-water habitats, and all other analyses of data reported herein were based on actual measured values. In total, missing data from five thermographs were replaced using this procedure (I.2, I.4, II.1, IV.1, and V.1), and the time period replaced never exceeded 1.5 months.

Principal component analysis

Correlation PCA (Thioulouse et al. 1997) was used to generate a habitat typology based on five thermal variables for the 3-week summer period. Correlation PCA standardizes all data by subtracting the mean and dividing by the standard deviation. Thermal variables included (*i*) average summer temperature, (*ii*) maximum rate of diel cooling, (*iii*) maximum rate of diel heating, (*iv*) maximum diel temperature pulse, and (*v*) Kamler's coefficient of daily thermal astatism (see Multiple linear regression section of Materials and methods).

Results

Environmental considerations

Long-term air temperatures (1938–1999) and precipitation (1923–1999) records indicated that 1998 and 1999 were within the range of long-term conditions (11.4–14.4°C and 1338–3104 mm, respectively). At ca. river-km 60 (220 m asl), annual average temperatures for 1998 and 1999 were 13.7 (minimum, –8.0°C; maximum, 39°C) and 14.0°C (minimum, –8.0°C; maximum, 35°C), respectively, and precipitation was 2059 and 1743 mm, respectively.

Stage heights in 1998 and 1999 were low compared with an 18-year (1982–1999) record. Arscott et al. (2000) reported that the average stage height has decreased over this time period, probably as a result of abstraction for agricultural and domestic uses. However, there is no discernable trend in yearly maximum stage height or flood frequency

Table 3. Average daily mean temperature (°C ± 1 standard deviation (SD); $n = 21$), maximum diel temperature amplitude (°C), and maximum rate of diel temperature change (°C·h) from 22 water bodies along the course of the Tagliamento River.

	Daily temperature		Maximum diel amplitude		Maximum rate of change	
Geomorphic unit or habitat description	Summer	Winter	Summer	Winter	Summer	Winter
I. Constrained headwater streams						
1. 2nd order	**10.4 ± 1.64**	**2.5 ± 0.87**	**6.9**	**2.3**	**4.3**	**1.3**
2. 2nd order	11.4 ± 1.45	1.5 ± 0.53	4.3	2.2	1.5	0.4
3. 2nd order	10.4 ± 1.77	1.9 ± 0.94	6.5	1.8	2.5	0.8
4. 3rd order	**11.2 ± 1.48**	**2.1 ± 0.67**	**5.4**	**1.5**	**2.3**	**0.6**
5. 4th order	**11.3 ± 1.59**	**2.0 ± 0.68**	**5.3**	**1.5**	**2.1**	**0.6**
II. Headwater island-braided flood plain						
1. 4th-order main channel	**10.6 ± 1.05**	**5.7 ± 0.35**	**3.7**	**0.7**	**1.8**	**0.3**
2. Alluvial channel	10.4 ± 0.44	6.3 ± 0.32	1.4	0.8	0.7	0.3
3. Alluvial channel	11.9 ± 0.59	5.6 ± 0.38	0.9	0.5	0.4	0.3
4. Alluvial channel	10.2 ± 0.30	6.7 ± 0.39	0.7	0.5	0.4	0.2
IV. Lower island-braided flood plain						
1. 7th-order main channel	**15.6 ± 1.65**	**7.8 ± 0.54**	**5.2**	**2.0**	**1.8**	**0.8**
2. Side channel	14.3 ± 1.25	8.3 ± 0.49	3.4	2.0	1.4	1.1
3. Backwater	14.6 ± 0.56	7.6 ± 0.57	2.6	2.2	1.2	1.0
4. Pool near main channel	22.1 ± 3.95	4.3 ± 0.40	6.9	1.1	2.5	0.5
5. Pool far from main channel	13.9 ± 0.59	6.0 ± 1.20	1.8	3.2	0.5	1.2
V. Braided-to-meandering transition flood plain						
1. 7th-order main channel	**18.9 ± 1.85**	**8.8 ± 0.52**	**5.8**	**1.8**	**2.1**	**0.6**
2. Backwater	15.3 ± 0.48	10.1 ± 0.80	2.9	3.0	1.5	1.4
3. Pool near main channel	17.2 ± 1.01	7.6 ± 0.65	3.0	1.7	1.9	0.6
4. Pool far from main channel	25.0 ± 2.70	6.4 ± 0.87	5.3	2.8	2.6	2.2
VI. Meandering flood plain						
1. 7th-order main channel	**17.1 ± 1.27**	nd	**4.8**	nd	**1.7**	nd
2. Backwater	18.0 ± 0.85	4.8 ± 0.29	2.6	1.2	1.2	0.5
3. Pool near main channel	25.9 ± 2.49	11.9 ± 0.45	6.0	1.2	1.9	0.6
4. Pool far from main channel	23.8 ± 1.42	5.3 ± 0.19	2.0	0.3	0.4	0.2

Note: Summer and winter values were calculated during 3-week periods (8–28 July or 1–21 December 1998). Values in bold type are from main channel habitats; all others are lateral water bodies. nd, no data.

over the period of record. Discharge from 1994–1997 averaged 41.5 $m^3 \cdot s^{-1}$ at a location at ca. river-km 68, with a maximum discharge of 1622 $m^3 \cdot s^{-1}$ occurring on 15 November 1996. In 1998, complete floodplain inundation occurred twice (both in autumn), but other flow pulses that reconnected floodplain habitats occurred frequently throughout the year. In 1999, complete floodplain inundation occurred once (in autumn); however, four other major flow pulses occurred (one in spring and three in autumn).

Thermal patterns in relation to the environment

The eight thermal variables could be separated into three distinct groups based on a priori expectations and Pearson product moment correlation analysis among dependent variables. Average daily temperature (group *a*), maximum diel amplitude (group *b*), and maximum rate of change (group *c*) are reported for each habitat in Table 3. In group *a*, average daily temperature was significantly correlated ($p < 0.05$) with minimum and maximum daily temperature and had correlation coefficients $r > 0.95$. In group *b*, average diel temperature pulse was significantly correlated ($p < 0.05$) with maximum diel temperature pulse and Kamler's coefficient and had correlation coefficients of $r = 0.99$ and 0.87, respectively. In group *c*, maximum rate of heating and cooling were significantly correlated ($p < 0.05$), with $r = 0.97$.

Forward stepwise multiple regression analysis was carried out for eight dependent temperature variables from all 22 habitats with eight geomorphic and environment variables (independent variables) for both summer and winter periods. Results of four of these regressions are presented in Table 4 with summer model statistics on the left and winter statistics on the right. Only four of the 16 regressions are reported in the table to avoid redundancy; however, the results from all regressions are reported herein. Of the 16 multiple regression analyses (8 temperature variables × 2 seasons), only one was not significant (winter maximum rate of cooling, Table 4). In every case, the summer period models extracted a greater number of model coefficients to explain the variance in the data matrix. The regression coefficients in Table 4, standardized and listed in descending order of explanatory power, are measures of the relative influence of the independent variable on the dependent variable.

Results of the multiple regression analyses for group *a* (average daily temperature (Table 4) and minimum and maximum temperatures (not in Table 4)) were similar and always had elevation (probably a direct predictor of air temperature) as the variable explaining the most variance in the model. The winter models always only consisted of elevation and azimuth; however, only the elevation regression coefficient was significant ($p < 0.001$). For the summer period, the minimum daily temperature model ($p < 0.001$ and $R^2 = 0.76$) extracted elevation, current velocity, slope, and width; how-

Table 4. Results from forward stepwise multiple regression analysis of summer (left side) and winter (right side) thermal variables.

Summer						Winter					
Source	df	*F*	*P*	Regression coefficients	R^2	Source	df	*F*	*P*	Regression coefficients	R^2
Average daily temperature											
Regression model	3	14.60	<0.001		0.71	Regression model	2	14.42	<0.001		0.62
Elevation			<0.001	–0.86		Elevation			<0.001	–0.83	
Azimuth			0.038	–0.32		Azimuth			0.254	0.18	
Maximum depth			0.125	–0.30		Residual	18				
Residual	18										
Maximum diel temperature pulse											
Regression model	5	3.81	0.018		0.54	Regression model	3	3.27	0.047		0.37
Azimuth			<0.001	–1.20		Slope			0.008	–0.77	
Slope			0.022	–0.63		Azimuth			0.027	–0.65	
Maximum depth			0.049	–0.55		Canopy			0.197	–0.27	
Current velocity			0.013	0.51		Residual	17				
Canopy			0.075	–0.45							
Residual	16										
Maximum rate of diel increase											
Regression model	6	10.30	<0.001		0.80	Regression model	5	3.89	0.018		0.56
Azimuth			<0.001	–0.95		Azimuth			0.003	–0.85	
Slope			0.003	–0.59		Slope			0.004	–0.81	
Specific conductance			0.003	0.48		Canopy			0.097	–0.36	
Elevation			0.022	0.46		Current velocity			0.200	–0.25	
Canopy			0.018	–0.42		Specific conductance			0.248	0.24	
Current velocity			0.309	0.14		Residual	15				
Residual	15										
Maximum rate of diel cooling											
Regression model	4	4.53	0.011		0.52	Regression model	3	2.78	0.073		
Azimuth			0.011	0.71		Model not significant					
Specific conductance			0.013	–0.54							
Slope			0.046	0.53							
Canopy			0.101	0.34							
Residual	17										

ever, none of the extracted variables was significant (except the intercept). The summer maximum daily temperature model ($p < 0.001$ and $R^2 = 0.68$) extracted elevation, azimuth, maximum depth, width, and canopy, and only elevation and azimuth were significant. Results for the average daily temperature are shown in Table 4.

Group *b* multiple regression analyses indicated that azimuth and slope were the most important factors explaining relative diel temperature pulse. The summer average diel temperature pulse (not shown in Table 4) model ($R^2 = 0.59$) extracted six variables (azimuth, current velocity, slope, canopy, maximum depth, and specific conductance); of these, azimuth and current velocity were significant ($p < 0.007$) and slope and canopy were marginal ($p = 0.067$ and 0.065, respectively). The winter model (not shown in Table 4) extracted slope and azimuth and both were significant ($p =$ 0.005 and 0.01, respectively); however, the correlation coefficient for the model was low ($R^2 = 0.39$). The three most predictive variables for both summer and winter Kamler's coefficient models (neither shown in Table 4), in order of variability explained, were azimuth, elevation, and slope (all $p \leq 0.01$), with the summer model also extracting current velocity ($p = 0.009$), specific conductance (not significant (ns)), and canopy (ns) and the winter model extracting maximum depth (ns). The winter model of Kamler's coefficient was the only winter model to have a better correlation coefficient than the summer counterpart ($R^2 = 0.86$ versus 0.85). Results for the maximum diel temperature pulse models are shown in Table 4.

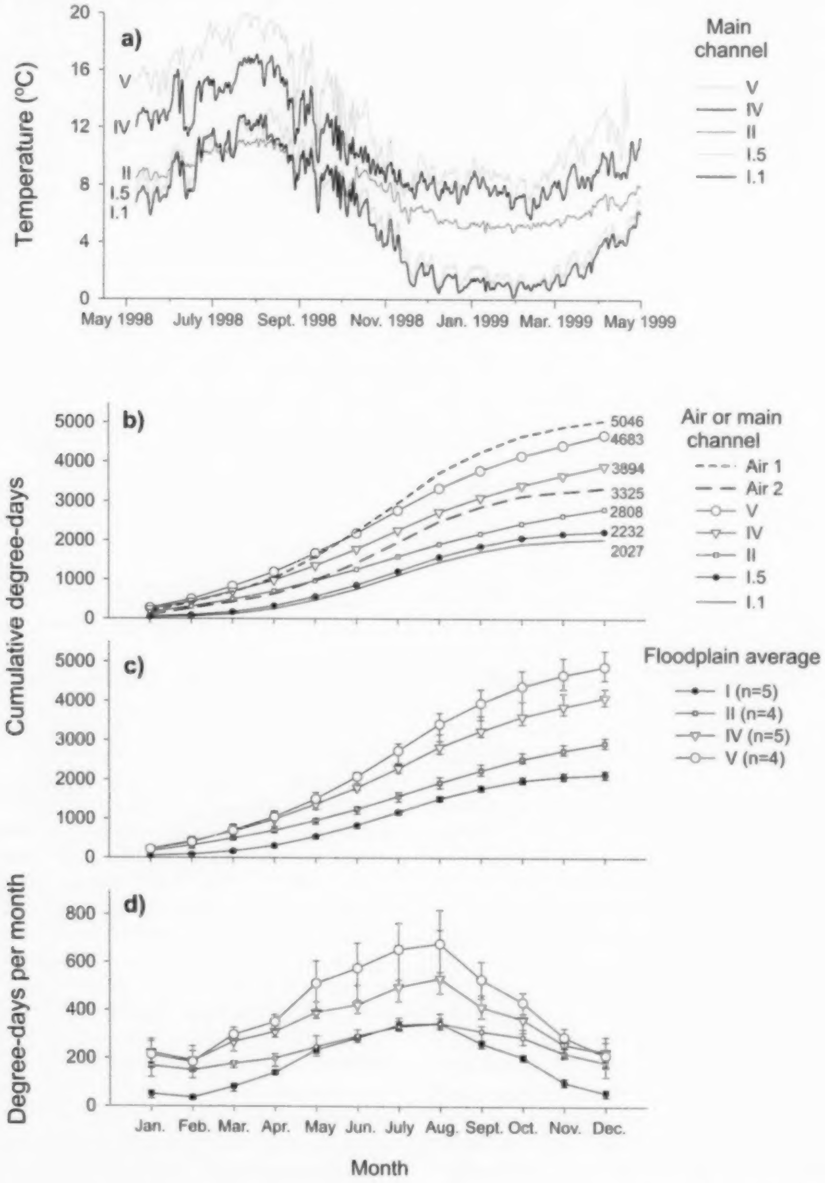
Group *c* variables were significantly ($p < 0.05$) correlated with those of group *b*. Azimuth and slope were the variables that explained the most variance in both the summer and winter models for maximum rate of diel temperature increase (Table 4); although in the summer model, specific conductance, elevation, and canopy were also significant regression coefficients. The correlation coefficient of the summer model of maximum rate of cooling was low ($R^2 = 0.52$). Azimuth, specific conductance, and slope were all variables that contributed significantly to this model. The winter model of maximum rate of cooling was not significant and therefore no model coefficients were reported (Table 4).

Degree-days

Seasonal and daily variation in temperature (Fig. 2*a* for main channel thermographs) determines spatial and temporal patterns of annual and monthly degree-days. Annual degree-days (Fig. 2*b*) along the main channel increased with decreasing elevation, with 2027 degree-days recorded for the 2nd-order (I.1) stream and 4683 in reach V. The 2nd-order (I.1) stream had the lowest annual degree-days despite having greater (but not significant) daily temperatures in summer than other habitats in reaches I or II.

Differences in daily average temperatures were reflected in the patterns of annual and monthly degree-days (Figs. 2*c*,

Fig. 2. (*a*) Daily average temperatures from the main channel of the Tagliamento River at five locations along the longitudinal continuum from May 1998 to July 1999. (*b*) The accumulation of degree-days at main channel locations (plus two air thermographs) over a 1-year cycle (January through April are from the 1999 calendar year, May through December are from the 1998 calendar year). The (*c*) cumulative or (*d*) monthly average degree-days per month (±1 standard deviation) for each of four study reaches. Average degree-days were calculated from 4 or 5 different water bodies within each reach (see Table 1 for habitat descriptions). Elevation is 220 m asl (meters above sea level) at Air 1 and 1000 m asl at Air 2.

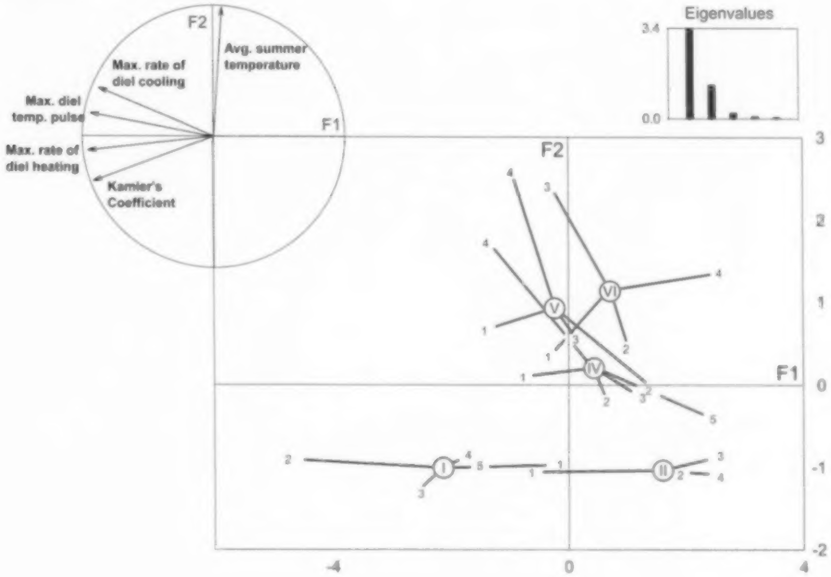


2*d*). Unfortunately, monthly and cumulative degree-days could only be calculated for 18 of the 22 habitats because of missing data. Variation of annual degree-days within a reach increased with decreasing elevation. Variation at the floodplain level in degree-days was largely a function of variation in summer, as was evident from comparing monthly degree-days (Fig. 2*d*). Winter temperatures were important for degree-days in reach II habitats and could be recognized by the relatively linear increase in cumulative monthly degree-days.

Habitat typology and thermal heterogeneity

The relationships between five summer thermal variables (average summer temperature, maximum rate of heating and cooling, maximum diel temperature pulse, and Kamler's coefficient) and 22 habitats were assessed using PCA (Fig. 3).

Fig. 3. Principal component analysis of the relationship between five thermal variables (correlation circle) and 22 floodplain water bodies (factor map) along the Tagliamento River corridor. The F1 (eigenvalue, 3.4; variance explained, 68%) and F2 (eigenvalue, 1.27; variance explained, 25%) axes explained 93% of the variation in the data matrix (inertia). In the factor map, the circles (with reach identifications) represent the average score for a floodplain reach and are connected by lines to actual scores for each habitat within the reach. Legend for habitats is identical to Fig. 2.

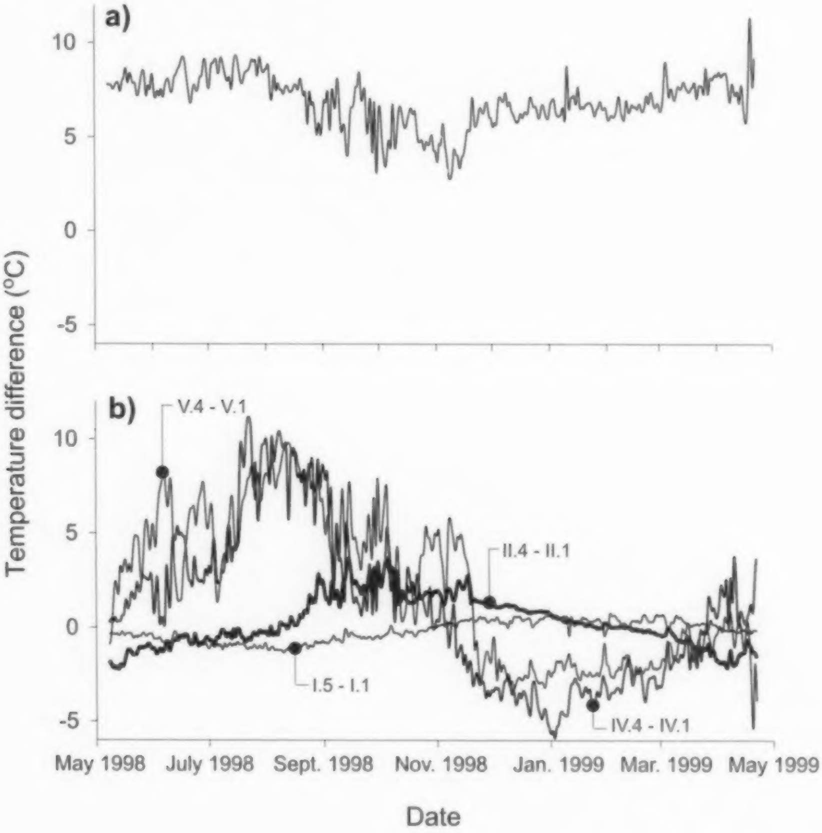


The first (68%) and second (25%) axes explained 93% of the variance in the data matrix. The first axis (F1) explained greater than 75% of the variation in maximum rate of diel heating and cooling, maximum diel temperature pulse, and Kamler's coefficient and was negatively correlated to all four variables. The second axis (F2) explained greater than 97% of the variation in average summer temperature. The separation in thermal variables by these two axes results in the distribution of habitats shown in Fig. 3. Reaches I and II were clearly separated from all other reaches owing to low temperatures (i.e., separation along the F2 axis and were separated from each other along the F1 axis resulting from differences in rates of heating and cooling and diel temperature pulses). Reaches IV, V, and VI were poorly separated by the PCA because of considerable overlap in both the F1 and F2 dimensions. Standing water bodies tended to be grouped to either the upper or right-hand portion of the two-dimensional space. Inspection of the habitat map revealed that main channels (all 1s in Fig. 3) tended to have average rates of diel thermal fluctuations and average temperatures within each of the floodplain reaches (i.e., II, IV, V, and VI). This illustrates that lateral water bodies can be either warmer or cooler than the main channel and can exhibit either greater or lesser diel fluctuations.

To compare thermal heterogeneity along the main channel of the Tagliamento with that across a single floodplain environment, differences in daily average temperatures between habitats for an entire year were calculated (Fig. 4). The difference between one of the lowest elevation habitats and the highest elevation habitat (reach V.1 minus reach I.2) for an entire year (May 1998 through April 1999) is plotted in Fig. 4*a*. This longitudinal temperature difference ranged from 4.0 to 11.5°C, with an average of 7.3°C. Additionally, this relationship was always positive (i.e., headwaters were always cooler than the lowland reach). To assess thermal heterogeneity across a flood plain, the daily average temperature of the habitat farthest from the main channel was subtracted from the daily average main channel temperatures in reaches I, II, and V. In reach IV, the second furthest habitat (IV.4) was used owing to insufficient data collected from the furthest habitat. These lateral temperature differences are illustrated in Fig. 4*b* and ranged from –5.9 to 11.1°C (reach IV) and averaged between 0.3°C and 2.1°C (reaches II and V, respectively).

To examine the influence of hydrology on thermal heterogeneity, maximum hourly differences in temperature between the coolest and warmest water body were plotted against the summer hydrograph (Fig. 5). Maximum thermal difference within reaches I and II were 3.7°C and 2.6°C, respectively, and remained relatively constant (despite diel changes) over the 2-month period, indicating a weak relationship between thermal heterogeneity and water level. In the lowland flood plains (reaches V and VI), maximum differences between the coolest and warmest water bodies were high (13.1°C and 14.8°C, respectively) and varied considerably over the summer period. In these reaches (V and VI), the pattern of thermal differences between water bodies exhibited an inverse relationship to the hydrograph. These patterns also occur when all water bodies are included in the analysis. For example, maximum hourly difference in temperature between the coolest and warmest water bodies correlated significantly ($p < 0.05$) with the coefficient of variation calculated for hourly temperature in all water bodies measured within a reach ($r^2 = 0.97$).

Fig. 4. (*a*) The daily difference in temperature between a lowland main channel habitat in reach V (V.1) and a headwater stream (I.1) from May 1998 to May 1999. (*b*) The difference in daily average temperature between habitats located laterally to the main channel and the main channel in reaches II, IV, and V and between the downstream habitat I.5 and the upstream habitat I.1 in reach I over the same time period. See Fig. 1 for habitat locations.



Discussion

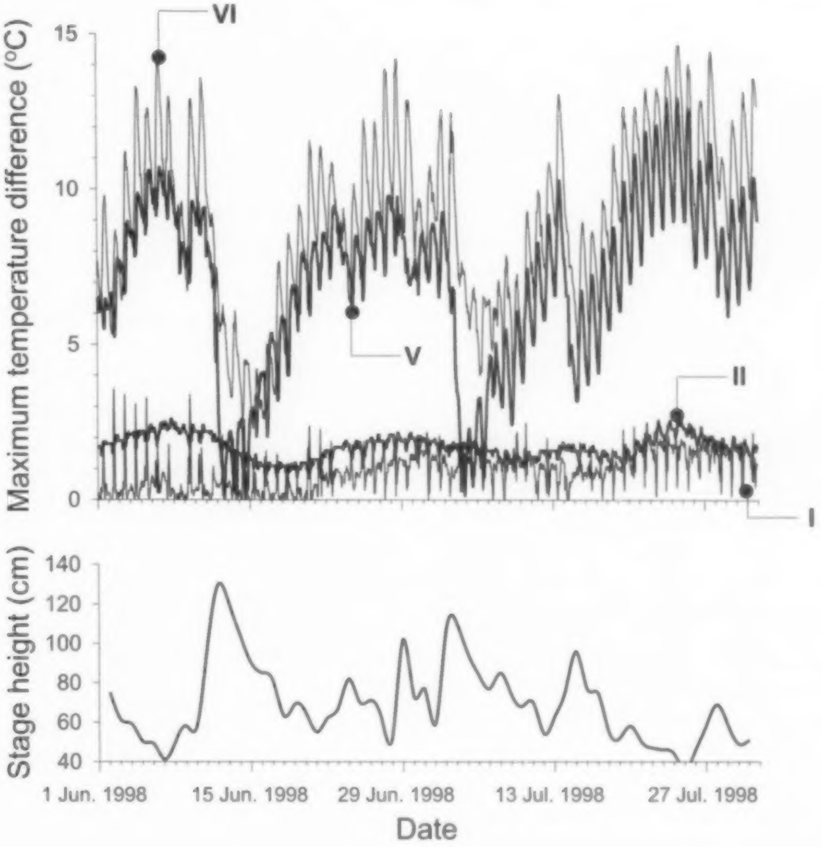
Longitudinal patterns

Longitudinal patterns of average daily, minimum, and maximum temperature were influenced primarily by elevation and secondarily by azimuth as suggested by multiple linear regression analysis. However, the progression of increasing temperature in the main channel with elevation was interrupted at two points along the continuum, at reaches II and VI. Both of these reaches were markedly influenced by upwelling groundwater (D.B. Arscott, personal observation) and had summer water temperatures in the main channel lower than upstream source waters. During winter months, these habitats were warmer than upstream sources (data for reach VI based on point measurements not presented herein (D.B. Arscott, unpublished data)).

Average and maximum diel temperature pulses, Kamler's coefficient of daily thermal astatism, and the maximum rates of heating and cooling were influenced primarily by floodplain azimuth and floodplain slope. This reflects the influence that floodplain orientation (azimuth) has on exposure to incoming radiation and how slope may influence heat exchange processes via turbulence (although also a correlate of elevation and therefore may reflect other mechanisms). Other local factors that were probably also important correlates of these thermal variables included groundwater exchange, degree of shading, and water volume. This conclusion was supported by the presence of maximum depth, current velocity, canopy, and specific conductance (as an indicator of degree of groundwater influence) as regression coefficients in the multiple regression models for each of these variables. Hawkins et al. (1997) found that temperatures of single-thread streams in northern California were most strongly related to channel morphology (% channel as a pool) and hydrology (current speed) rather than elevation and azimuth. Further, they reported that riparian shading in these mountain streams was related to maximum daily temperature and daily temperature range. In our analyses of longitudinal thermal patterns, different thermal variables were influenced by different environmental factors. Although elevation and azimuth had a primary role influencing temperature magnitude, local factors such as channel morphology (maximum depth and slope), degree of shading (% canopy), and hydrology (current speed) were important factors related to diel pulses and rates of temperature change.

In contrast to the longitudinal pattern of maximum diel

Fig. 5. The maximum difference in hourly temperature between the coolest and warmest water body in reaches I, II, V, and VI and stage height (cm) at river-km 84 (below reach IV) for the time period 1 June to 1 August 1998. Habitats used for each comparison were I.1 and I.2, II.3 and II.4, V.2 and V.4, and VI.1 and VI.3. Average stage height in 1998 was ~80 cm (minimum, 0 cm; maximum, 300 cm).



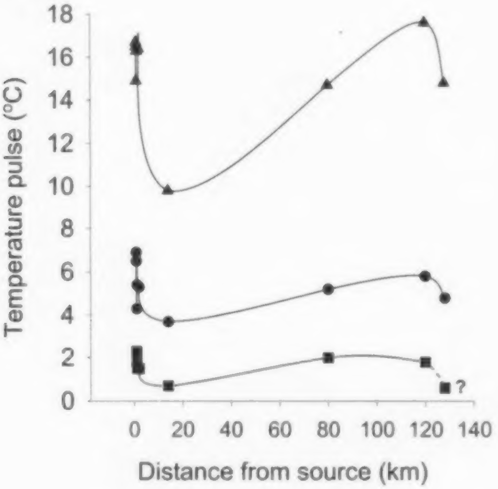
temperature pulse reported by Vannote and Sweeney (1980), the maximum diel temperature pulse at main channel locations along the Tagliamento river occurred in a 2nd-order headwater stream (Fig. 6). This was surprising because canopy cover at the data logger was high (90%). However, orientation (azimuth = 35) was conducive to high thermal input and the upper slope of the catchment was open (i.e., minimal forest cover). The lowest maximum diel temperature pulse was observed in a 4th-order headwater flood plain (reach II), probably owing to interactions with subsurface waters. Poole and Berman (2001) point out that the relative magnitude of the temperature pulse is a function of a stream's buffering capacity for heat, suggesting that daily (summer and winter) and annual pulses should follow the same relative patterns. We observed this for our study habitats; for example, in winter the pattern of diel temperature pulse (Fig. 6) and the longitudinal pattern in annual temperature pulse were nearly identical to the pattern (not magnitude) observed for the summer diel temperature pulse. Groundwater and a cool-water tributary were the likely cause of significant diel and annual temperature pulse attenuation in reaches II and VI, respectively.

Influence of subsurface flow paths was pronounced in the headwater island-braided flood plain (reach II). Immediately upstream of reach II, all surface water at base flow infiltrates into an alluvial aquifer and flows subsurface for ~3 km. Average temperature, diel pulse, and rate of temperature change (both heating and cooling) were considerably attenuated compared with other reaches for all habitats.

Thermal heterogeneity and the lateral dimension

Floodplain (lateral) thermal heterogeneity along the Tagliamento River corridor increased with decreasing elevation and floodplain development. The presence of standing water bodies in the flood plains of the lower reaches dramatically increased floodplain thermal heterogeneity. When lateral temperature differences are superimposed on longitudinal temperature difference, it is apparent that instantaneous temperature difference between habitats in lower flood plains can equal or exceed that occurring in the main channel along the entire river corridor. The range in summer maximum temperature observed on a single day in these lower flood plains was nearly 15°C between cool-water and warm-water habitats (reach V.3, 16.3°C; reach V.4, 31.1°C), whereas maximum temperature difference among habitats in reaches I and II was only 3–4°C. In these standing water bodies (backwaters and isolated water bodies), average

Fig. 6. Maximum diel (summer, circles; winter, squares) or annual (triangles) temperature pulse from nine main-channel habitats along the course of the Tagliamento River. Diel values were measured during a 3-week period in summer and a 3-week period in winter (winter measurement from habitat at river-km 127 is estimated).



summer temperatures could be either warmer or cooler than main channel environments depending on the degree of connectivity with interstitial waters (phreatic and hyporheic). Differing degrees of thermal stratification within these pools may also contribute to thermal variability. Cavallo (1997) showed that thermal stratification in floodplain ponds in alluvial rivers resulted in vertical thermal variation between 14°C (pond bottom) and 22°C (pond surface). Although no such data are presented herein, thermal stratification has been documented in pools located in reach IV (D. van der Nat, Department of Limnology, EAWAG, Dübendorf, Switzerland, unpublished data).

The influence of geomorphology and hydrology in determining spatiotemporal patterns of variation is particularly important at the floodplain scale and is responsible for floodplain form and function that create a variety of habitat types. Perhaps the most important attribute of lowland flood plains leading to lateral habitat heterogeneity along the Tagliamento River is the abundance of standing water bodies, which are present though rare in headwaters. Standing water bodies are responsible for much of the variation in chemical conditions across the Tagliamento (Arscott et al. 2000) and are also important structures contributing to floodplain thermal variation. This is particularly evident in temporal changes in temperature as a result of changing water level. As water levels increased, the temperatures in diverse habitats converged with main channel temperatures. As water level decreased, their temperatures diverged as water bodies became more and more hydrologically isolated. Thermal response time of a water body depended on its hydrological proximity to the main channel environment. In a pool near the main channel (reach VI.3), there was an abrupt and immediate drop in temperature each time the hydrograph increased, indicating a strong subsurface connection with the main channel. In a pool far from the main channel (reach VI.4), there was a 5-day time lag in the temperature response to an increasing hydrograph (see fig. 6 in Arscott et al. 2000).

The Flood Pulse Concept (Junk et al. 1989) described, among other things, the influence of flooding on abiotic factors and biotic communities in floodplain rivers. The homogenization of certain environmental conditions in water bodies located lateral to a river's main channel as a result of overbank flooding (depending on intensity and duration) has been well documented, particularly with regard to solutes and biota (Hamilton and Lewis 1987; Knowlton and Jones 1997; Lesack et al. 1998). With regard to aquatic thermal conditions, however, there is a paucity of information on the influence of flooding. Moreover, reports on thermal heterogeneity at the floodplain scale are nearly nonexistent (with exception of Mosley (1983), Tockner et al. (2000), and Malard et al. (2001)).

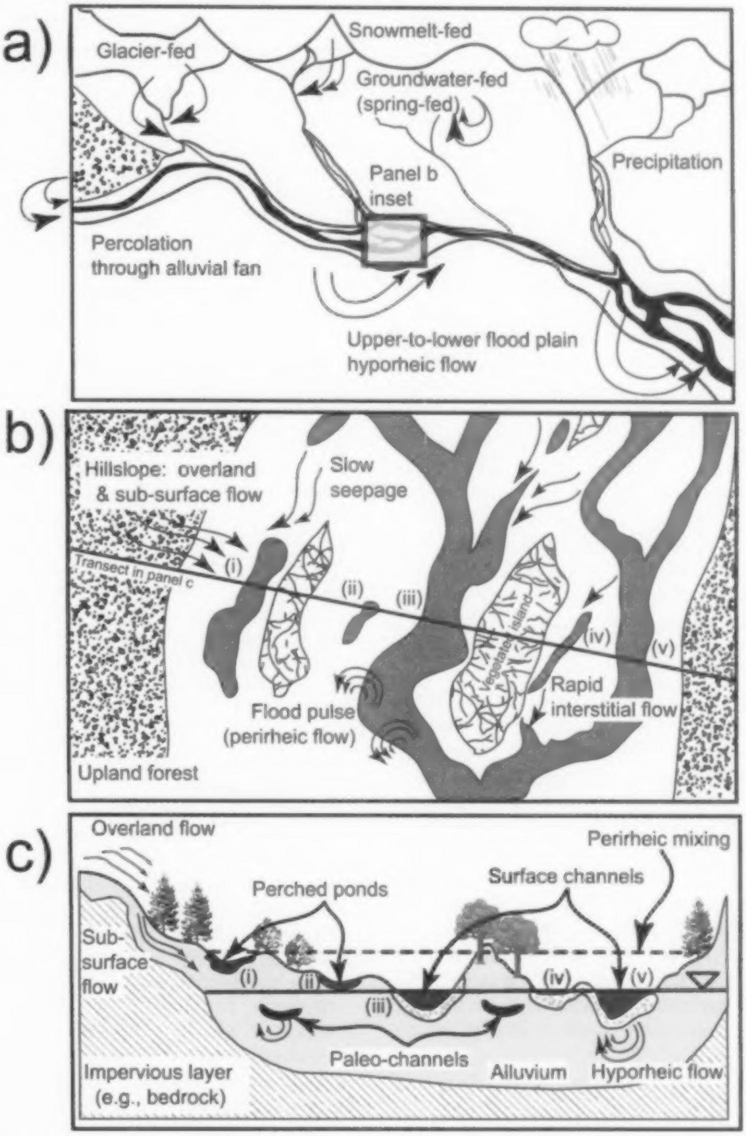
The downstream increase in thermal heterogeneity leads to a greater variation in monthly and average thermal degree-days in lower flood plains. Although variation across a flood plain in monthly thermal degree-days was higher in summer than in winter, this should not overshadow the importance of winter temperatures. For example, although summer daily temperatures in the headwater streams (reach I) were not significantly different from those of habitats in the headwater flood plain (reach II), greater winter temperatures in reach II accounted for annual degree-days that were nearly 1.5 times greater (2226 versus 3118).

Finally, the attempt to create a channel typology based on thermal variables using PCA separated habitats based on average summer temperature (F2) and rates of thermal change (F1). There was a clear distinction of headwater habitats (reaches I and II) from other reaches based on average summer temperature. Separation of these two reaches from each other occurred as the result of considerable differences in rates of heating and cooling, diel temperature pulse, and Kamler's coefficient. In contrast, the lower flood plains overlapped considerably in both summer temperature and rates of change. Flowing-water habitats grouped close together and standing water bodies exhibited large variation in both dimensions, apparently as the result of differential degrees of connectivity with alluvial aquifers. However, the contribution of differences among habitats in vertical thermal stratification cannot be ruled out as an additional source of variation.

The Tagliamento River represents one of the last morphologically intact river corridors draining the European Alps (Ward et al. 1999). The unconstrained nature and frequent inundation of its flood plains maintains a complex network of channels, backwaters, and isolated water bodies that change continuously in both time and space. The river exhibits distinct downstream changes in river morphology (Gurnell et al. 2000) and climate that influence physicochemical conditions (Arscott et al. 2000). Increasing water level as the result of precipitation events can influence channel-shifting processes and connects isolated water bodies causing drastic changes in environmental conditions. Many of the factors (i.e., hydrological regime, channel shifting, sediment transport) operating on a large scale in the Tagliamento River have been severely attenuated in other rivers by anthropogenic impacts.

It is important to superimpose later temperature variability

Fig. 7. Schematics of (*a*) catchment, (*b*) reach, and (*c*) floodplain cross section showing major flow paths influencing water temperature. Aquatic habitats in reach-scale schematic (*b*) designated *i–vi* are also indicated in cross-sectional schematic (*c*) and refer to ponds sealed with fine sediments (*i* and *ii*), a subsurface connected alluvial channel (*iv*), and surface channels (*iii* and *v*).


a)
Glacier-fed
Snowmelt-fed
Groundwater-fed
(spring-fed)
Precipitation
Panel b
inset
Percolation
through alluvial fan
Upper-to-lower flood plain
hyporheic flow
b)
Hillslope: overland
& sub-surface flow
Slow
seepage
Transect in panel c
(i)
(ii)
(iii)
(iv)
(v)
Vegetated island
Rapid
interstitial flow
Flood pulse
(perirheic flow)
Upland forest
c)
Overland flow
Perirheic mixing
Surface channels
Perched ponds
Sub-
surface
flow
(i)
(ii)
(iii)
(iv)
(v)
Paleo-channels
Alluvium
Hyporheic flow
Impervious layer
(e.g., bedrock)

across single flood plains upon longitudinal temperature gradients to provide a holistic perspective of thermal heterogeneity in river corridors. Along the Tagliamento River, maximum thermal heterogeneity occurred in lower reaches. Local geomorphological characteristics that interact with hydrology to generate and maintain a diversity of aquatic habitats (e.g., side channels, backwaters, and isolated pools) strongly influenced downstream patterns. In addition, factors that influence surface and subsurface flow paths (e.g., sediment structure, lateral inputs of hillslope runoff, and groundwater upwelling zones) modify local thermal regimes.

Manifestations of geomorphic influence on thermal patterns can be viewed at the scales of catchment (Fig. 7*a*), reach (Fig. 7*b*), and channel cross section (Fig. 7*c*). At the catchment scale, source waters (glacial, snowmelt, precipitation, phreatic) and large-scale percolation of water through soils and alluvium can each contribute to characteristic thermal patterns. Reach-scale factors, such as the distribution of sediments, can influence preferential flow paths thereby either isolating (e.g., perched ponds) or connecting, to differing degrees, phreatic and surface waters (via paleochannels and hyporheic flow). This determines the influence of groundwater and atmospheric processes on thermal regime within a habitat.

The flood pulse (overland flow resulting from groundwater saturation or overbank flooding) creates another type of mixing zone, the perirheic zone (sensu Mertes 1997), where channel water, pond water, groundwater, and direct precipitation mix together for short or long time periods (depending on catchment water retention character and presence–absence of different water sources). Flow pulses (sensu Tockner et al. 2000) describe more gradual water level changes resulting in expansion and contraction of channels and water bodies below bankfull. Flow pulses are especially important for temporary habitats such as ephemeral ponds or channels. During small increases in the water table, channel length increases, backwaters widen, and ponds begin to connect and flow. For a water body that is warmer than adjacent flowing surface waters (i.e., isolated from hyporheic flow), the result of a flow pulse might be a cooling effect (bringing the pond into equilibrium with channel temperatures) and attenuation of the ponds diel temperature pulse (volume-dependent factors). For a colder water body (well shaded and connected to cool phreatic waters), an increase in interstitial flows might improve subsurface–surface connectivity and thereby mix warmer waters from surface channels.

The floodplain cross section (Fig. 7*c*) helps emphasize the diversity of processes occurring across a single flood plain. Upland ponds, intermittently connected channels, paleochannels, and surface channels all can have vastly differing thermal regimes. In addition, habitats similar in geomorphology may differ markedly owing to local variables (e.g., vegetation, large wood debris, proximity to hillslope or main channel). Therefore, there is potential across a single flood plain for a multitude of thermal regimes depending on structural complexity.

Thermal patterns along intact, well-connected river corridors are complex and heterogeneous. Multiple factors at multiple scales work in concert to produce thermal variation in rivers, and the influence of environmental variables on this variation shifts spatially and temporally over both short and long time periods. Factors that determine temperature regimes in rivers may manifest at regional scales (climate, latitude, altitude, and continentality); however, local influences of geomorphology and hydrology are key variables influencing habitat-scale thermal regimes. A greater appreciation of thermal heterogeneity in river systems will undoubtedly lead to a better understanding of the role of temperature in the evolutionary ecology and conservation of aquatic biota as well as in the management of rivers and streams as important natural resources.

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Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory sea lamprey (*Petromyzon marinus*)

Lance A. Vrieze and Peter W. Sorensen

Abstract: This study used large laboratory mazes and natural stream waters to test the role of olfactory cues, including a pheromone released by larvae, in spawning stream localization by migratory sea lamprey (*Petromyzon marinus*). We found that migratory lamprey strongly prefer stream water over lake water and that this response is dependent upon a functional olfactory system. Responses persisted among migratory lamprey even after stream water was diluted a thousand times but were not seen among non-migratory lamprey. Experiments using waters from five streams demonstrated that a larval pheromone is a key determinant of stream attractiveness: water from streams with larval populations were consistently more attractive than those without, and adding larval odor to the latter reversed this relationship. Larval odor was attractive at low, realistic concentrations, especially when presented together with natural stream water, suggesting that streams contain other odors that synergize the actions of the pheromone. Some, but not all, of the activity of the larval pheromone could be explained by two bile acids released by larvae (petromyzonol sulfate and allocholic acid). Together, these results strongly suggest that migratory lamprey locate streams using a larval pheromone. This cue could be useful in lamprey control.

Résumé : De grands labyrinthes de laboratoire et de l'eau de ruisseaux naturels nous ont servi à vérifier le rôle des signaux olfactifs et, en particulier, d'une phéromone émise par les larves dans la localisation des ruisseaux de fraye chez la Grande Lamproie marine migratrice, *Petromyzon marinus*. Les lamproies migratrices préfèrent de beaucoup l'eau de ruisseau à l'eau de lac et cette réaction nécessite une système olfactif fonctionnel. La préférence demeure même après que l'eau de ruisseau ait été diluée 1000 fois; elle ne s'observe cependant pas chez les lamproies non-migratrices. Des expériences utilisant l'eau de cinq ruisseaux démontrent qu'une phéromone larvaire est le déterminant principal de l'attraction exercée par les ruisseaux; les eaux provenant de ruisseaux qui contiennent des populations de larves sont toujours plus attractives que les eaux des ruisseaux qui n'en ont pas et l'addition d'odeur larvaires à ces dernières inverse la relation. L'odeur larvaire possède un pouvoir d'attraction à des concentrations faibles et réalistes, particulièrement lorsqu'elle est présentée dans de l'eau naturelle de ruisseau, ce qui laisse croire que les ruisseaux contiennent des autres odeurs qui agissent en synergie avec la phéromone. Une partie, mais pas l'ensemble de l'activité de la phéromone larvaire, s'explique par l'émission de deux acides biliaires, le sulfate de pétromyzonol et l'acide allocholique, par les larves. Dans leur ensemble, ces observations tendent à indiquer clairement que les lamproies migratrices retrouvent les ruisseaux à l'aide d'une phéromone larvaire. Cette phéromone pourrait s'avérer utile dans le contrôle des lamproies.

[Traduit par la Rédaction]

Introduction

A variety of studies suggest that migratory fish commonly use olfactory cues to locate streams from oceans or lakes (Dodson and Leggett 1974; Doving et al. 1985; Stabell 1992). Although some species, such as Pacific salmon, appear to imprint to complex mixtures of compounds as juveniles (Hasler and Scholz 1983; Dittman et al. 1996; Shoji et al. 2000), others appear to recognize streams using innately recognized cues that correlate with habitat quality. Small inorganic ions such as calcium (Bodznick 1978), larger organic compounds associated with microbial decay (Sorensen 1986; Tosi and Sola 1993), and pheromones (Miles 1968; Nordeng 1977; Li et al. 1995) have all been suggested to serve as innately recognized cues. Of these, pheromones have garnered the most attention. However, although studies have shown that some species of migratory fishes are attracted to the odor of conspecifics (Miles 1968; Quinn and Tolson 1986; Keefe and Winn 1991), the precise significance of these odors remains unclear, because when conspecific odors have been tested against natural stream waters at realistic concentrations, their potency has appeared low (Brannon et al. 1984; Sorensen 1986; Brannon and Quinn 1990). Understanding pheromonal function has also been

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complicated by a lack of understanding of the identities of the cues involved. Recently, biochemical, physiological, and behavioral studies have suggested that migratory sea lamprey (*Petromyzon marinus*) use conspecific cues comprised of bile acids to locate spawning streams (Li et al. 1995; Bjerselius et al. 2000; Polkinghorne et al. 2001), creating an excellent opportunity to test the role of a pheromone in fish migration.

Sea lamprey are an ancient, jawless fish with a parasitic life history. They invaded the Great Lakes from the Atlantic Ocean in the first half of the 20th century with disastrous results on native fish communities (Smith and Tibbles 1980). Although the use of larval toxicants has remedied this situation to some extent, new control strategies for sea lamprey are actively sought. Sea lamprey start life as filter-feeding larvae (ammocoetes) burrowed into the sediments of freshwater streams. In the Great Lakes Basin, larvae metamorphose into a parasitic phase after 3–7 years (Purvis 1980) and migrate downstream into lakes where they parasitize other fish. After 12–16 months (Bergstedt and Swink 1995), they stop feeding, begin to sexually mature, and seek out streams up which they then migrate, spawn, and die. Notably, sea lamprey are selective in their choice of spawning streams and spawn in less than 10% of Great Lake tributaries (Morman et al. 1980). Because adult lamprey exhibit no tendency to return to natal streams (Bergstedt and Seelye 1995), it appears that they select streams using innately recognized cues.

The hypothesis that lamprey use a pheromone to locate spawning streams originated with the observation that the number of migratory adults captured in a stream often drops dramatically the year after ammocoetes are removed from the stream by larvicide treatment (Moore and Schleen 1980). Early behavioral studies conducted by Teeter (1980) using a small laboratory maze suggested that larval odor was attractive. More recently, two unique bile acids, petromyzonol sulfate (PS) and allocholic acid (ACA), have been implicated as components of the larval pheromone. Electrophysiological studies of the lamprey's olfactory system have found it to be extremely and specifically sensitive to both PS and ACA (Li et al. 1995; Li and Sorensen 1997), which it detects at concentrations ranging down to between 10^{-12} and 10^{-13} M. This threshold is within the range of bile acid concentrations estimated to exist in Great Lakes' streams based on larval bile acid release rates (Polkinghorne et al. 2001).

Most recently, a series of four experiments has demonstrated that larval holding water and the bile acids contained therein stimulate swimming in captive migrants (Bjerselius et al. 2000). Animals caught early in their migration shifted their distribution towards the side of a small laboratory maze containing larval odor in one experiment and increased their swimming activity when exposed to larval odor in another. In two other laboratory experiments, migratory lamprey increased their activity in areas of an experimental tank containing the larval bile acids. Although all four experiments describe positive results and support the migratory pheromone hypothesis, the preferences appeared relatively weak. Further, these experiments did not assess the attractiveness of natural stream waters or the pheromone's role within the context of a stream's complex chemical makeup. The latter is important because lamprey could be using more than a single cue contained within or associated with stream water. If a pheromone were found to have a major influence on the attractiveness of stream waters to lamprey, it might prove useful in lamprey control.

The objectives of the present study were to determine (*i*) whether and how migratory sea lamprey are attracted to the odor of natural stream waters; (*ii*) the significance of the larval pheromone in determining the attractiveness of stream waters; and (*iii*) the significance of larval bile acids in determining the attractiveness of the larval pheromone. Our experiments were conducted in the laboratory as a prelude to more complex and expensive field tests.

Materials and methods

Experimental design

Experiments were conducted at the Hammond Bay Biological Station (HBBS), Millersburg, Michigan, between May and July of 1996–1999. Our assay attempted to simulate conditions encountered by lacustrine sea lamprey approaching river mouths. Recently captured migratory animals were tested during their period of peak activity (at night in the spring) in a pair of identical mazes supplied with Lake Huron water obtained from a deep offshore intake. They were offered the choice of two slowly flowing waters with temperatures slightly exceeding that of lake water. Here, we describe the basic parameters of the design. Details are found in Vrieze (1999).

Migratory lamprey were captured in traps located in Cheboygan, Ocqueoc, and Manistique rivers in Michigan and St. Mary's River in Ontario, transported to HBBS, and then acclimated to Lake Huron water for at least 1 day. Except for Experiment 1*d*, no attempt was made to separate lamprey from different locations (this experiment showed that it made no difference). Only females (46.8 ± 3.9 cm (mean ± standard deviation), $n = 310$) were tested because males were needed for other experiments and Bjerselius et al. (2000) found that both sexes responded to larval odor in the same manner. Animals were maturing but had not ovulated and had a Gonadal–Somatic Index (gonad weight/body weight × 100%) that increased from about 17% to 26% each year. Individuals ($N = 1444$) were used only once and were tested within 21 days of capture.

Two identical test mazes were constructed from Plexiglas panels positioned within indoor concrete raceways (Fig. 1). Raceways were supplied with Lake Huron water at a rate of about 500 $L{\cdot}min^{-1}$ to produce a velocity of 2–5 $cm{\cdot}s^{-1}$ and a water depth of about 15 cm. Lake water temperature varied between 5 and 21°C depending on the time of year. Each maze measured 9.0 m × 1.8 m and possessed a release area located upstream of a test area, the latter of which offered animals the choice of entering one of two side channels down which different experimental waters were added using pumps pulsed on and off approximately every 15 s (for all experiments except for Experiment 2*d*). Tests using dye found experimental waters to be completely mixed with lake water by the time they reached the bottom of the side channels, and dilutions given herein assume complete mixing.

Experiments used waters from five streams in the vicinity of HBBS (Fig. 2; Table 1). Three streams contained sea lamprey ammocoetes (Ocqueoc River, Cheboygan River, and Schmidt Creek), whereas two streams (Nagel Creek and Lone Pine Creek) have not contained ammocoetes of any lamprey species in their 40-year monitoring history (S. Morkert, Ludington Biological Station, Ludington, Mich., personal communication). Both Nagel Creek and Lone Pine Creek are small, but they are large enough to attract migratory smelt (*Osmerus mordax*) and white suckers (*Catastomus commersoni*; personal observations) and are larger than some streams historically used by sea lamprey (Morman et al. 1980). Stream waters needed for a night's experiment were collected that

Fig. 1. The maze used to test the preferences of migratory sea lampreys. The test area was divided into three channels, a central channel connecting it with the release area of the maze and two side choice channels. Lake Huron water was pumped into the upstream end. Stream waters, larval holding water, and bile acids were mixed with Lake Huron water at the upstream end of each side channel. Distribution was monitored in the upstream sections of the side channels and in the downstream section (stippling) in Experiment 1. Activity was monitored in each side channel by counting the number of times that lamprey crossed three lines drawn in each side channel (small-dashed lines). The large-dashed lines represent plastic screening.

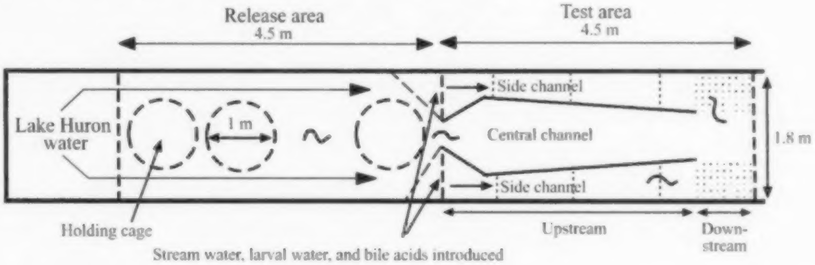
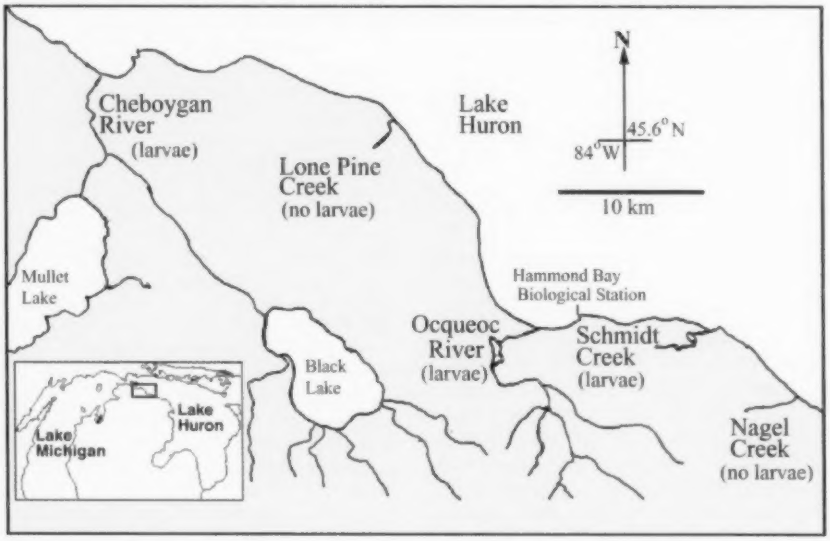


Fig. 2. Locations of the five streams from which waters were taken for use in the experiments. The Cheboygan River, Ocqueoc River, and Schmidt Creek contained sea lamprey ammocoetes. Lone Pine Creek and Nagel Creek did not contain ammocoetes of any species of lamprey. The Hammond Bay Biological Station is located at the inshore end of its inlet pipe, pictured.



day with a gas-powered pump, transported to the biological station, and held in insulated holding tanks. For experiments using only Lake Huron water in one side channel, a holding tank was filled with Lake Huron water. The temperatures of waters in the holding tanks were brought to within 0.1°C of each other and were made approximately 0.5°C warmer than the raceway Lake Huron water after mixing.

At least 5 h before each experiment, groups of four lamprey were placed into four holding cages located in the release area of each maze. Most experiments used 16 groups of four lamprey and extended over four nights. All experiments were conducted in complete darkness starting at least 1 h after sunset and continuing until 2:00 AM. For each trial, a group of lamprey was released by raising its holding cage and observed for 20 min using overhead infrared lights (780 nm; beyond the range of lamprey vision; Harosi and Kleinschmidt 1993) and cameras connected to a video recorder in another room. At the end of each trial, lamprey were captured by net and returned to their cages. Trials were separated by 15 min. The specific channels to which test stimuli were added were alternated between nights, creating a balanced design.

Trials were scored by watching a video monitor as they occurred or by reviewing videotapes at a later time. Experiment 1 monitored both activity and distribution in each channel, whereas the remaining tests examined distribution only because it was thought to be most relevant to stream location and was strongly correlated with activity (see Results). Distribution was monitored by noting the positions of lamprey within specific sections of the test area (central or side channels) every 30 s during the test period. Activity was assessed in Experiment 1 by counting the number of times that lamprey crossed lines drawn on the floors of both side channels. Preferences for experimental waters were assessed by calculating relative percent time spent in each side channel (observations in one side channel divided by the total number of observations in both channels, × 100). Percent time was then arc-sine transformed to meet the assumptions of parametric analysis, and mean distribution was compared with 50% (expected value) using a two-tailed one-sample *t* test (Zar 1984). Trials for which groups of animals spent an average of less than 25% of their time in the test area were not used (32 of 361 trials were disqualified). Preferences were rated as weak ($P < 0.10$), strong ($P < 0.05$), or very strong ($P < 0.01$). For presentation, means and 95% confidence intervals were back-transformed following Zar (1984).

Experiment 1: determining whether and how migratory lamprey are attracted to the odor of natural stream waters

Experiment 1a. Is the odor of water from a stream that contains a population of larval lamprey attractive to migratory sea lamprey?

We reasoned that if lacustrine lamprey use a larval pheromone to locate spawning streams, then migratory lamprey placed in the maze should choose to enter river water if given the choice between it and lake water. Further, this choice should be made on the basis of olfactory cues (odor). The first experiment, conducted in 1996, addressed both issues. Lamprey were subjected to one of two treatments: (*i*) olfactory blocking in which lampreys' nasopores were filled with a fast-setting, inert dental impression material (3M Express, St. Paul, Minn.), which pilot studies showed to have no effect on lamprey health, and (*ii*) a sham control in which lampreys' nasopores were filled with water-soluble teleost gelatin (Sigma, St. Louis, Mo.), which was expelled by lamprey. A day after being treated, groups of control and anosmic lamprey were offered the choice of diluted Cheboygan River or Lake Huron water. The Cheboygan River was used because it contains many ammocoetes and attracts migratory sea lamprey each spring (Fig. 2; Table 1). It was diluted into one side channel at a rate of 1 part per 33 parts of lake water, a concentration that we have measured in river plumes up to 0.5 km offshore in Lake Huron (P.W. Sorensen and L.A. Vrieze, unpublished results). As a control, Lake Huron water was collected at the same time as Cheboygan River water, stored in an identical tank, brought to the same temperature, and then added at an equivalent rate to the other side channel. For this initial experiment, movement patterns were assessed by noting the distribution of animals, tracing the paths of lamprey, and counting how often they crossed lines drawn across the channels (Fig. 1).

Experiment 1b. Is lamprey stream water attractive because it stimulates upstream swimming?

This experiment, conducted in 1997, sought to confirm the attractive properties of stream water and to assess whether attraction to it is associated with an increased tendency to swim upstream, a possible response to a migratory cue (Bjerselius et al. 2000). This test used water from the Ocqueoc River, another stream near HBBS that contains many ammocoetes and attracts migratory lamprey (Fig. 2; Table 1). For this experiment, river water was added to one side channel and stored Lake Huron water was added to the other. Each was added at a rate sufficient to produce a 1:40 dilution in fresh lake water. For analysis, distribution and swimming activity were examined in all three channels, which were subdivided into upstream and downstream sections (Fig. 1) to permit a more detailed understanding of how lamprey responded to stream water.

Experiment 1c. Is stream water attractive at the low concentrations that lamprey encounter at river mouths?

This question was addressed in a series of experiments conducted in 1998 that tested progressively lower concentrations of river water. Ocqueoc River water was tested at dilutions of 1:200, 1:2000, and 1:20 000 in lake water. Stored lake water was diluted to the same extent in the other side channel as a control. For this and all subsequent experiments, we examined only time spent in the upstream sections of the side channels because Experiment 1*b* found lamprey to spend most of their time in these regions and that distribution reflected activity (see Results).

Experiment 1d. Are the preferences of sea lamprey the same irrespective of collection site?

If the larval pheromone is a primary determinant of the attractiveness of river water, then responses to it should be uniform and innate; lamprey collected from different locations should have the same preferences. We tested this possibility in 1997 by conducting a pair of matched experiments, simultaneously evaluating the preferences of migratory sea lamprey caught in either the Cheboygan River or the Ocqueoc River, offering each the choice of water from these two rivers at a dilution of 1:40. This experiment validated our use of lamprey from multiple locations.

Experiment 1e. Are only migratory-phase sea lamprey attracted to stream water?

To confirm that responses to river waters reflected migratory behavior, we tested the responses of parasitic lamprey (27.7 ± 5.5 cm; $n = 48$) to Ocqueoc River water at a dilution of 1:40. This experiment was conducted in 1997 and used stored lake water as a control in the opposite channel. Parasitic-phase lamprey feeding on fish were collected by local fishermen. Because of their small size, animals were released from smaller holding cages placed in the central channel of the test area. Plastic netting was placed across the upstream end of the central channel.

Experiment 2: determining the significance of larval odor as a pheromonal attractant within stream waters

Experiment 2a. Are waters from streams with larval populations naturally more attractive than those lacking larvae?

If the larval pheromone is a principal component of stream odor recognized by migratory lamprey, then we reasoned that waters collected from streams that contain populations of larvae should be more attractive than those that do not. We tested this possibility by evaluating the preferences of sea lamprey offered the choice of waters from streams that either possessed or lacked larval lamprey (of any species). Three comparisons using five streams located near HBBS were performed in 1997–1998 (Fig. 2). First, water from the Cheboygan River (a lamprey stream) was compared with water from Lone Pine Creek (a non-lamprey stream), at equivalent concentrations (1:40 in lake water). Next, we compared water from another lamprey stream (Ocqueoc River) with that of another non-lamprey stream (Nagel Creek) with lamprey stream water being diluted twice as much (1:80) as the non-lamprey stream water. A third test compared water from the smallest lamprey stream (Schmidt Creek) with the largest non-lamprey stream (Nagel Creek), which were located 10 km apart. Water samples from these streams were collected in 1998 and analyzed by the University of Minnesota Soil Analysis Laboratory.

Experiment 2b. Is larval odor attractive, and if so, can adding it to water from a non-lamprey stream make the latter as attractive as water from a lamprey stream?

This experiment used larval holding water to directly assess the importance of larval odor in stream waters. First, we tested the effects of adding larval odor to water from a non-lamprey stream (Nagel Creek). Larval odor was produced following the protocol used previously to both assess the behavioral effects of larval odor in well water (Bjerselius et al. 2000) and study bile acid release (Polkinghorne et al. 2001). Briefly, a population of 1000 larval sea lamprey was maintained in a 350-L Fiberglas tank containing sand. An identical tank with sand only was maintained as a control. Before behavior experiments, bakers' yeast was added to both tanks (feeding stimulates bile acid release; Polkinghorne et al. 2001) and incoming water was turned off. The control tank received one-third as much yeast to approximate the amount left uneaten by larvae in the other tank. Water was collected for tests 1 day later. In the first experiment (1997), larval holding water was tested at a concentration similar to that used by Bjerselius et al. (2000). Water from the larval and control tanks was pumped into the lake water (in opposite channels) at a rate of 1:28, while Nagel Creek water was simultaneously added at a rate of 1:40 into both channels (thus

Table 1. Biological and chemical characteristics of natural stream and lake waters used in preference tests.

Water source	Larval densities[a]	Adult sea lamprey caught[b]	Flow[c] $(m^3 \cdot s^{-1})$	Total organic carbon $(mg \cdot L^{-1})$	$CaCO_3$ $(mg \cdot L^{-1})$	Measurable elements[d] $(mg \cdot L^{-1})$					
						P	Fe	Na	K	Ca	Mg
Cheboygan River	700 000+	22 941	24	4.8	86	0.18	0.04	4.7	0.85	49	13
Lone Pine Creek	None	No trap	0.006	20.9	108	0.19	0.21	1.2	0.78	41	13
Ocqueoc River	450 000+	9 836	2.8	7.6	109	0.20	0.13	2.7	0.72	56	14
Schmidt Creek	10 000	No trap	0.11	14.3	125	0.14	0.11	2.3	<0.7	45	12
Nagel Creek	None	No trap	0.013	16.6	155	0.17	0.33	3.9	0.72	61	16
Lake Huron	—	—	—	1.8	65	0.19	0.03	4.4	1.1	31	9

[a] 1996 population estimates for larval sea lamprey based on fisheries surveys (Klar et al. 1997, 1999). The Cheboygan and Ocqueoc rivers have significant but unmeasured populations of native lamprey. The absence of larvae in Lone Pine and Nagel creeks is based on repeated surveys over 40 years (S. Morkert, USFWS, Ludington Biological Station, Ludington, Mich., personal communication).

[b] Number captured in stream traps for 1997 (Schleen et al. 1998). Adults have never been reported in the Nagel or Lone Pine creeks, which are not routinely trapped.

[c] Mean annual discharge of Cheboygan and Ocqueoc rivers from Schleen et al. (1998). Values for Nagel, Lone Pine, and Schmidt creeks measured by the authors at time of normal late-spring discharge.

[d] The following elements and compounds were below detection limits in all samples: Al, Cu, B, Pb, Ni, Cr, Cd, and PO_4.

producing a final dilution of 1.4 parts larval or control odor to 1 part Nagel Creek water to 40 parts lake water).

We next asked if larval odor was adequate to explain the preference of lamprey for water from a lamprey stream over water from a non-lamprey stream. In other words, could the relative potencies of river waters be altered by simply adding larval odor to water from relatively unattractive streams? Cheboygan River was again tested against Lone Pine Creek except that this time control water was added to the former and larval holding water to the latter (both at a 1:29 dilution rate). River waters were added to lake water at a rate to produce the 1:40 dilution tested earlier. This experiment was conducted in 1997 immediately after Experiment 2*a*, so a direct comparison was possible.

Experiment 2c. Is larval odor attractive at concentrations low enough to account for the natural attractiveness of lamprey stream waters?

Here we determined how low of a concentration of larval odor attracts migratory sea lamprey and whether it approximates that naturally found in lamprey streams. In Experiment 2*b*, we had tested larval odor at dilutions of 1:28; now we tested dilutions of 1:10 000 and 1:100 000 (meaning 100 mL of holding water was added to 10 000 L of lake water). Water from a control tank with sand only was added as a control to the opposite channel, while Nagel Creek water was used as a background odor at a 1:50 dilution rate in both channels. For these experiments, conducted in 1999, holding water was tested 12 h after water inflow into the holding tanks was shut off.

Experiment 2d. Is the pheromone complimented by other odorous cues in stream water?

Although the previous experiments indicated that the larval pheromone played a key role in stream attraction, they did not address the possibility that other biologically significant odors might exist in streams. We tested this possibility with two experiments. First, in 1997, we ascertained whether natural cues not associated with larvae might have a role in stream attraction. Nagel Creek water (at a dilution of 1:40) was added to one side channel and stored Lake Huron water was added to the other. Next, we tested whether the activity of the larval pheromone might be enhanced by the presence of non-pheromonal odors found in the "background", a phenomenon frequently seen with insect pheromones and termed "synergism" (Landolt and Phillips 1997). A matched set of tests was conducted in 1998: the first tested larval odor in a background of lake water only; the second tested larval holding water in a background of non-lamprey stream water (as performed in previous experiments). In these experiments, larval odor and its control were prepared in the same manner as described in Experiment 2*b* and added at a rate of 1 part holding water to 117 parts lake water to opposite channels. In addition, the first test added stored lake water (at a rate that resulted in a 1:240 dilution in background lake water) down each side channel, whereas the second test added Nagel Creek water to both side channels at the same rate. This set of experiments was conducted over the same nights using the same larval holding waters.

Experiment 3: determining the significance of larval bile acids within the larval pheromone

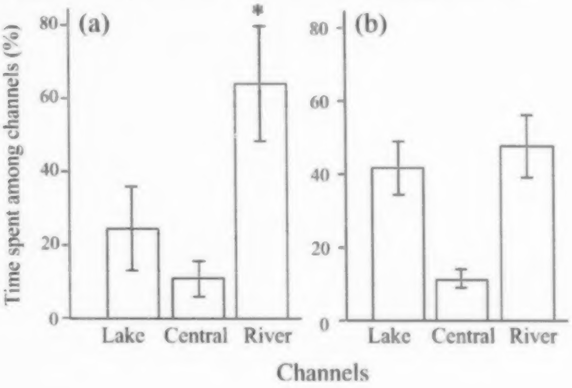
Experiment 3a. Do larval bile acids make stream waters more attractive?

Although larval bile acids have been shown to be mildly attractive in well water (Bjerselius et al. 2000), their potency had not yet been evaluated within the context of natural stream waters. Here we tested this three times. In all three instances, stream waters were added at a rate of 1:40 into both side channels, while methanol control (the carrier for the bile acids) was added to one and a mixture of PS and ACA was added to the other. Lone Pine Creek water was used for the stream water background in 1997 and Nagel Creek water was used in 1997 and 1999. Bile acids were added at a rate to produce concentrations of 1×10^{-10} M for PS and 0.15×10^{-10} M for ACA, concentrations measured by Polkinghorne et al. (2001) in larval release waters and thought to exist in some streams. PS was obtained from gall bladders and purified by HPLC (Li. et al. 1995), whereas ACA was synthesized (Toronto Research Chemicals, North York, Ont.).

Experiment 3b. Do larval bile acids account for all of the activity of "whole" larval odor?

Noting that attraction to bile acids seemed weaker than responses observed earlier to larval holding water in Experiment 2, we wondered if larval holding water might contain compounds in addition to PS and ACA. To test this possibility, we compared the potency of larval holding water to bile acids. For this test, conducted in 1999, Nagel Creek water was pumped into both side channels at a dilution rate of 1:50 while a mixture of PS and ACA was added to one channel and larval holding water was added to the other. Larval holding water was created as described in Experiment 2 and added at a rate that produced a final dilution of 1:10 000, whereas PS and ACA were added at the rates used in Experiment 3*a*. Samples of larval holding water were saved and their bile acid content was assayed by liquid chromatography – mass spectrometry (LC–MS).

Fig. 3. Distribution results from Experiment 1*a*: mean percent time (and 95% confidence interval) spent by (*a*) sham-treated migratory sea lamprey (n = 7 groups of 4 animals) and (*b*) anosmic migratory sea lamprey (10 groups of 4) in the three channels when Cheboygan River water was introduced into one side channel and Lake Huron water was introduced into the other. Time spent in the central channel was small (10–15% of total time in test section of the maze) and was not evaluated. Preferences were determined by calculating the percentage of the total time spent in each of the side channels and comparing it with the expected value of 50% if distribution was otherwise equal (one-sample t test; *, $P < 0.05$; only increases shown).



Results

Experiment 1: determining whether and how migratory lamprey are attracted to the odor of natural stream waters

In Experiment 1*a*, most sea lamprey (3.3 ± 0.3 animals per trial) swam downstream into the test section of the maze. Those with functional olfactory systems then spent approximately twice as much of their time in the Cheboygan River side channel as they did in the lake water side channel ($P < 0.05$; Fig. 3*a*). Anosmic (olfactory-blocked) animals also swam into the test section of the maze at a similar rate ($P > 0.10$), but they spent equal amounts of time in the river and lake water side channels ($P > 0.10$; Fig. 3*b*). Sham and anosmic lamprey spent little time in the central channel. Examining the movement patterns of individual lamprey, we found that sham-treated animals tended to follow the edge of the river water channel and downstream edge of the test area, giving them an "L"-shaped swimming pattern. In contrast, anosomic animals spent equal amounts of time following the edges of all areas, resulting in a "U"-shaped swimming pattern (Fig. 4). No difference in total swimming activity was seen between anosmic or sham-treated animals (total number of line crossings per trial for sham-treated was 279 ± 43 vs. 251 ± 36 for anosmic animals; $P > 0.10$), with 75.6 ± 6.5% of the activity of the sham animals being in river water versus only 56.9 ± 5.2% for anosmic lamprey.

When lamprey were offered the choice of Ocqueoc River water versus Lake Huron water in Experiment 1*b*, lamprey once again showed a strong preference for river water ($P < 0.01$; Fig. 5). Dividing the channels into upstream and downstream sections, we found that lamprey spent nearly all of

Fig. 4. Activity results from Experiment 1*a*: path of movement of representative (*a*) sham-treated and (*b*) anosmic sea lamprey offered the choice between Cheboygan River water and Lake Huron water.

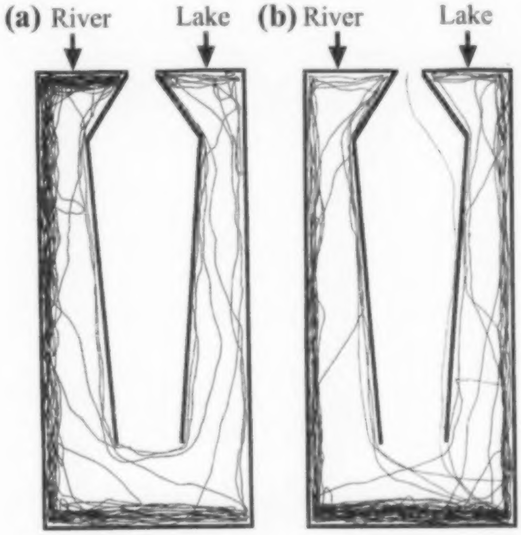


Fig. 5. Results of Experiment 1*b*: mean percent time spent by migratory lamprey (±95% confidence interval) among the three channels when offered Ocqueoc River water and Lake Huron water (n = 15 groups of 4 animals). Side channels were divided into upstream (open bars) and downstream (stippled bars) sections as shown in Fig. 1. Preferences were determined by calculating the percentage of the total time spent in the upstream portion of both side channels attributable to the time spent in the upstream portion of the river water channel and comparing with the expected value of 50% (one-sample t test; **, $P < 0.01$; only increases shown).

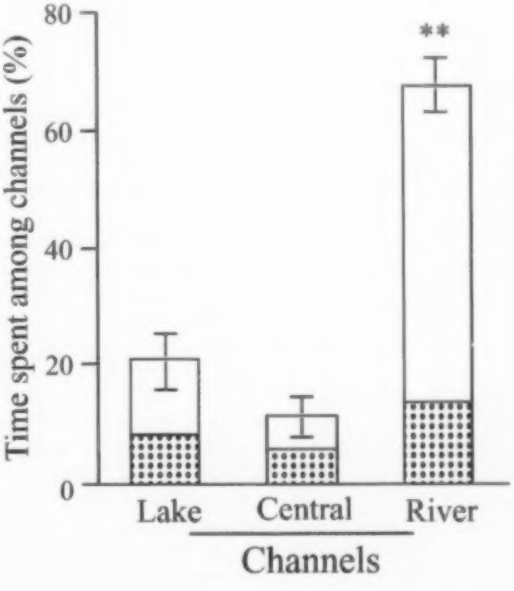
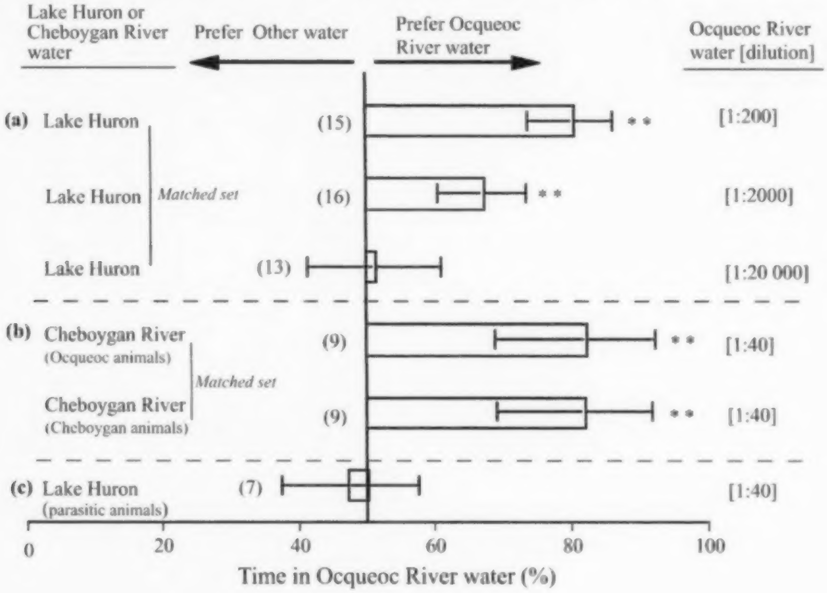


Fig. 6. Results of Experiments 1*c*, 1*d*, and 1*e*: mean percent time (±95% confidence interval) spent by migratory sea lamprey in Ocqueoc River water versus either Lake Huron or Cheboygan River ("Other") water. (*a*) Lake water versus Ocqueoc River diluted to three different extents (Experiment 1*c*). (*b*) Cheboygan River water tested versus Ocqueoc River water twice, once using lamprey captured in the Ocqueoc River, the other using Cheboygan River animals (Experiment 1*d*). (*c*) Lake water tested versus Ocqueoc River water using parasitic animals (Experiment 1*e*). Numbers in parentheses are the number of groups tested (4 animals per group). A "matched set" means that the experiments were conducted using animals and waters from similar collection times. Results of individual experiments are compared to the expected value of 50% by one-sample *t* test: **, $P < 0.01$.



their time in the river water channel in its upstream section (78.6 ± 3.2%), whereas in the lake water side channel, they spent only about half of their time in its upstream section (59.2 ± 4.7%; Fig. 5; $P < 0.01$, unpaired *t* test). Lamprey spent less than 10% of their time in the central lake channel. Swimming activity closely paralleled lamprey distribution with 71.7 ± 2.4% of all line crossings being noted in the river water channel. Based on these findings, all future analyses described distribution in the upstream sections of the side channels only.

In Experiments 1*c*, 1*d*, and 1*e*, river water was found to be highly attractive to migratory lamprey but not to parasitic-phase lamprey. In Experiment 1*c*, lamprey were found to spend significantly more time in river water than in lake water when it was diluted 200 and 2000 times ($P < 0.01$) but not 20 000 times ($P > 0.10$; Fig. 6*a*). Preference decreased with concentration. Comparisons of the relative potencies of Ocqueoc River and Cheboygan River water in Experiment 1*d* found that lamprey collected from both locations strongly preferred Ocqueoc River water ($P < 0.01$) and to similar extents ($P > 0.10$; Fig. 6*b*). Parasitic lamprey showed no preference for river water ($P > 0.10$; Fig. 6*c*).

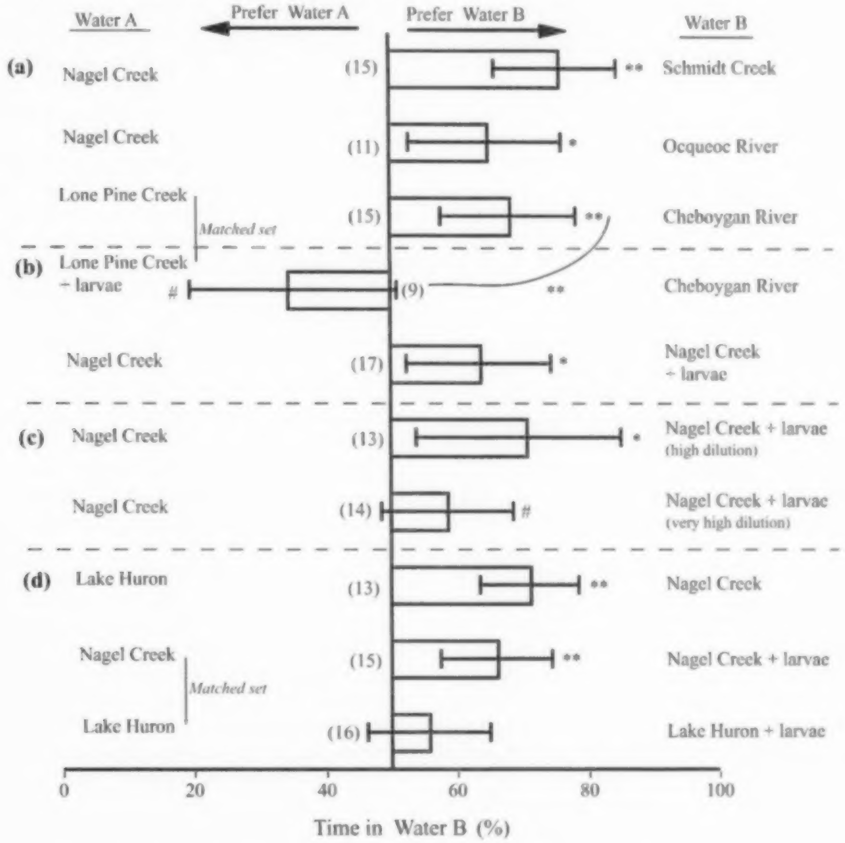
Experiment 2: determining the significance of larval odor as a pheromonal attractant in stream water

In Experiment 2*a*, water from streams with larvae was compared with water collected from streams lacking larval populations on three occasions. In the first test, lamprey strongly preferred ($P < 0.01$) water collected from the Cheboygan River, which contains larvae, to water from Lone Pine Creek, which did not (Fig. 7*a*). A similar result was seen in the second test when lamprey preferred Ocqueoc River over Nagel Creek water ($P < 0.05$; Fig. 7*a*) even though the former was diluted twice as much with lake water. Finally, when waters from the smallest streams were compared, lamprey were once again found to select water from the system with larvae (Schmidt Creek) over one without (Nagel Creek) ($P < 0.01$; Fig. 7*a*). Chemical analysis found no clear relationship between ion composition and attraction, although the two non-lamprey streams had the smallest flows and highest levels of total organic carbon and iron (Table 1).

In Experiments 2*b* and 2*c*, larval holding water was found to be highly attractive when tested in several ways. In Experiment 2*b*, a relatively high concentration of larval holding water in the background of water from a non-lamprey (Nagel Creek) stream was tested and found to be strongly preferred over the stream water alone ($P < 0.05$; Fig. 7*b*). In Experiment 2*b*, it was also found that adding larval holding water to Lone Pine Creek, a non-lamprey stream, made this water more attractive than that of the Cheboygan River, a lamprey stream ($P < 0.10$; Fig. 7*b*), reversing the normal relative attractiveness of these river waters ($P < 0.01$). In Experiment 2*c*, migratory lamprey were still attracted to larval holding water when it was diluted 10 000 times (high dilution; $P < 0.05$) and weakly attracted when it was diluted 100 000 times (very high dilution; $P < 0.10$) (Fig. 7*c*).

Results of Experiment 2*d* suggested that the larval phero-

Fig. 7. Results of Experiment 2: mean percent time (±95% confidence interval) spent by migratory sea lamprey in various combinations of natural stream, lake, and larval holding waters. (*a*) Two streams lacking populations of larvae ("Water A") versus three streams with larvae ("Water B"; Experiment 2*a*). (*b*) A stream lacking larvae to which larval holding water had been added ("Water A") versus a stream naturally containing larvae ("Water B"; Experiment 2*b*). This experiment was carried out at the same time as the last experiment from 2*a*. (*c*) Non-lamprey stream water ("Water A") versus the same stream water to which two different amounts of larval holding water had been added ("Water B"; Experiment 2*c*). (*d*) Three experiments assessing the role of odors not released by larvae (Experiment 2*d*). In the first, lake water is tested versus water from a non-lamprey stream (Nagel Creek). The second and third are a matched set of experiments that test Nagel Creek water versus Nagel Creek water plus larval holding water and then Lake Huron water versus lake water plus larval holding water. Concentrations are described in the text. Numbers in parentheses denote the number of groups of 4 animals tested. Results of individual experiments are compared to 50% by one-sample *t* test, whereas matched experiments were compared by two-sample *t* test: #, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$.



mone is complemented by other stream odors. First, water from a non-lamprey stream (Nagel Creek) was found to be more attractive to lamprey than Lake Huron water on its own ($P < 0.01$; Fig. 7*d*). Next, in a test of synergism, larval holding water was found to be not attractive ($P > 0.10$) when tested in (and against) lake water but highly attractive when tested in (and against) a background of Nagel Creek water diluted into lake water ($P < 0.01$; Fig. 7*d*).

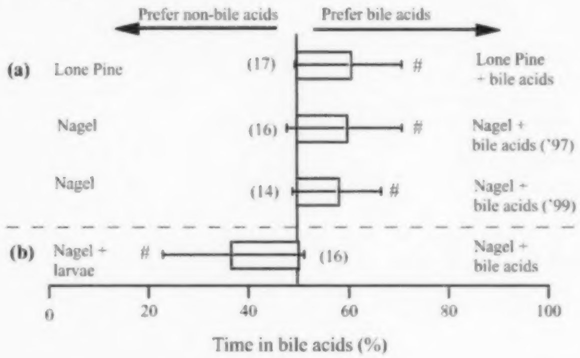
Experiment 3: determining the significance of bile acids in the larval pheromone

In Experiment 3*a*, the larval bile acids PS and ACA were weakly attractive to migratory sea lamprey all three times they were tested in a background of Nagel Creek or Lone Pine Creek water ($P < 0.10$; Fig. 8*a*). When larval holding water was compared directly with bile acids in Experiment 3*b*, lamprey showed a weak preference for larval holding water over bile acids ($P < 0.10$; Fig. 8*b*). When larval holding waters were analyzed by LC–MS, PS and ACA concentrations were found to be approximately 20 000 times less than when PS and ACA were tested alone.

Discussion

Taken as a whole, our experiments demonstrate that the odor of natural stream waters is highly attractive to migratory sea lamprey at very low concentrations and that a pheromone released by larval sea lamprey is a critical part of this odor. Particularly interesting is the finding that stream waters vary in their attractiveness and that their potency directly correlates with the presence of larval odor. The activity of this pheromone appears to be synergized by other

Fig. 8. Results of Experiment 3: mean percent time (±95% confidence interval) spent by migratory sea lamprey in (*a*) Lone Pine Creek or Nagel Creek (non-lamprey stream) water versus the same water into which petromyzonol sulfate (PS) and allocholic acid (ACA) were added (Experiment 3*a*) and (*b*) Nagel Creek water to which larval holding water had been added versus Nagel Creek water to which PS and ACA had been added (Experiment 3*b*). Numbers in parentheses denote the number of groups of 4 animals tested. Results of individual experiments are compared to 50% by one-sample *t* test; #, $P < 0.10$.



as yet unidentified compounds found in natural stream waters that also have some activity of their own. Our experiments also demonstrate that PS and ACA are important components of the larval pheromone but that other components exist. These findings complement earlier field studies that show a relationship between larval abundance and adult capture records (Moore and Schleen 1980) and laboratory studies demonstrating that PS and ACA are released by larvae (Polkinghorne et al. 2001) and that adults respond to them at relevant concentrations (Li et al. 1995; Bjerselius et al. 2000).

Our demonstration that streams with larval populations tend to be particularly attractive to migratory lamprey strongly suggests that the larval pheromone is an important facet of stream selection. That larvae residing in these streams are largely responsible for the attractive nature of stream odor is directly corroborated by our finding that the relative potencies of stream waters could be reversed by simply adding larval odor to one of them. Evidence for this phenomenon is also found in the field where analyses of adult capture rates find them to decrease dramatically in streams after their larvae have been removed by larvicide application (Moore and Schleen 1980). It is also not uncommon for adult lamprey to cease returning to small streams once the larvae have been extirpated (Torblaa and Westman 1980). Although the non-lamprey streams that we studied were relatively small and had high levels of iron and total organic carbon, we believe that these factors had little role in their lack of attractiveness. First, we found lamprey to prefer water from the Ocqueoc River to the Cheboygan River, in spite of the fact the Ocqueoc River had much higher concentrations of iron and organic carbon. Second, we were able to make non-lamprey streams highly attractive simply by adding very small amounts of larval holding waters to them. Third, we used activated carbon to extract organic compounds from stream water, leaving the ions behind, and found the extracted waters to have no behavioral activity (Vrieze 1999). Together, these data strongly suggest that streams with larval populations are more attractive because of a larval pheromone and that this attribute naturally serves to attract migratory lampreys to them.

The potency of larval holding water was high and within the range of that expected of a long-distance migratory attractant. We found that larval holding water from tanks with as few as 3 larvae·L^{-1} were highly attractive when diluted as much as 10 000 times into dilute river water. Although a true threshold was not reached, it likely is in the vicinity of a 1:100 000 dilution, which we found to be only weakly (although consistently) attractive. The latter dilution is approximately 1000 times lower than that tested by Teeter (1980) and establishes that larval odor is potent enough to naturally serve as a migratory cue: 1000 larval lamprey are adequate to activate a moderately sized stream with a discharge of 1 $m^3 \cdot s^{-1}$. This is a common density for sea lamprey larvae in many Great Lakes streams (Klar et al. 1999), and if native species of lamprey also release this pheromone (a possibility yet to be ascertained), then many streams should be extremely attractive because of larval odor alone. The results of this study may be the only example of a putative migratory pheromone for which activity has been verified at low, natural concentrations within a natural stream water background.

Although our study used a laboratory maze, we believe that it represents a valid measure of migratory behavior and pheromonal attraction for several reasons. First, attraction to stream water was not seen among non-migratory parasitic lamprey. Second, the behavior noted (increased rates of swimming into flowing water scented with river or larval odors) seems reasonable for a migratory behavior and resembles that noted earlier in an assay conducted in a stream (Bjerselius et al. 2000). Third, the close association seen between attraction and increased swimming activity is similar to that described by Bjerselius et al. (2000), who also found that sexually mature adults did not respond to larval odor. Fourth, although we did not test responses of lamprey to other fish odors as a control, the migratory lamprey tested were no longer feeding and thus presumably would not have been responding to prey odors. In summary, it seems reasonable to conclude that the observed increases in the attractiveness of stream waters to adult lamprey after the addition of small quantities of larval odor is associated with migratory attraction. Field tests are, of course, now needed to ascertain how the behaviors that we observed in the laboratory relate to actual behaviors of free-ranging lamprey searching for streams in lakes or oceans.

This paper suggests that two lamprey bile acids, PS and ACA, are components of the migratory pheromone. These compounds, which we know to be produced and detected by sea lamprey, were weakly but consistently attractive at low concentrations when added to water from streams lacking lamprey. Other experiments (Bjerselius et al. 2000) have also shown PS and ACA to elicit moderate levels of upstream swimming in well water. Although all of these results are positive, the direct test of these compounds against larval holding water conducted in this study suggests that additional pheromonal components most likely exist. Similarly, the sensitivity of the lamprey olfactory system to PS as measured by EOG recording (threshold of about 10^{-13} M) is not able to explain why Ocqueoc River water (which likely contains 10^{-11} M to 10^{-12} M PS; P.W. Sorensen, unpublished data) remained attractive when diluted about 2000-fold in the maze, even if, as some of our unpublished data suggest, EOG underestimates behavioral sensitivity by a factor of 10. Nevertheless, these bile acids can explain enough of the attractiveness of river waters to be biologically relevant as we have found that river waters may only be diluted to about half of their original concentration within 0.5 km of river mouths. Of course, until we know the complete identity of the pheromone, the role of mixtures within it, and the concentrations of the pheromone that lacustrine lamprey normally encounter as they search for rivers, the precise role of PS and ACA is difficult to assess. As a first step in the process, we are presently attempting to elucidate the number of unknown components in the larval pheromone.

A novel finding of this study is that natural stream waters contain odorous compounds that both have activity on their own and enhance the activity of the larval pheromone. Thus, Nagel Creek water was more attractive than lake water, and when larval holding water was added to it, larval odor became more attractive than it had been when presented with lake water only. Tests of Lone Pine Creek water have found it also to be attractive (L.A. Vrieze and P.W. Sorensen, unpublished data). The existence of synergism between natural stream odors and larval odor likely explains the weak responses seen by Bjerselius et al. (2000) to larval holding water when tested in a well-water background in circular test tanks. Although the larval pheromone may be the first known example of pheromonal synergism with environmental odors in a vertebrate, this phenomenon is relatively common among phytophagous insects which are often most attracted to sexual or aggregation pheromones when found in a background of host plant odor (Landolt and Phillips 1997). A seemingly analogous situation to that of lamprey is found in the *Culex* mosquito, which deposits eggs in water and whose oviposition pheromone is synergized by the odor of unknown organics found in nutrient-rich waters (Mboera et al. 1999). That a biologically relevant background odor can synergize the activity of a conspecific odor with which it is normally associated makes biological sense and in no way compromises our ability to consider such an odor a pheromone. Rather, by demonstrating that biologically relevant concentrations of larval lamprey odor have potent, adaptive, and innate effects on the behavior of migratory phase conspecifics that are mediated by the olfactory system, we have confirmed that this stimulus fulfills the requirements of a pheromone (Sorensen and Wyatt 2000).

Although it is unclear exactly what function non-pheromonal odors might play in stream location, the fact that streams that have never been known to attract lamprey from lakes possess this odor suggests that its role is permissive. Thus, whenever we added larval odor to a stream water (this study) or it has been removed with larvicide treatment (Moore and Schleen 1980), the effects on stream attractiveness have been dramatic. To draw an analogy, these findings suggest that the pheromone may function as a "trump" card in determining which streams migratory lacustrine lamprey will eventually enter as they encounter a variety of otherwise similar streams in their search for spawning habitat. Accordingly, although we believe that multiple factors may influence stream selection by migratory lamprey, we suggest that the larval pheromone is likely of greatest importance. Nevertheless, it is possible that non-pheromonal odors may play a role in stream selection such as during the time when the Great Lakes were first being colonized by lamprey. If identified, these non-pheromonal odors might be used to enhance activity in a pheromonal control program.

It is now clear that sea lamprey, like other migratory fishes (Smith 1985; Sorensen and Caprio 1998), use olfactory cues to locate spawning streams. Sea lamprey in which olfactory systems had been blocked were not attracted to river waters in our maze. This laboratory finding is strongly supported by a field study that released approximately 200 nose-plugged and sham-treated lamprey in Lake Huron 1 km from the Ocqueoc River. Nearly half of the sham-treated animals found a river, but less than 10% of the anosmic animals did (L.A. Vrieze and P.W. Sorensen, unpublished data). Similarly, we have found that extracting river waters with activated charcoal to remove organic (odorous) compounds makes them unattractive (Vrieze 1999). Olfaction may not be the only sensory modality involved in stream finding, but it is a critical one.

The discovery that river water can be diluted over 1000 times before losing potency suggests that it is capable of serving as a natural attractant in lakes. Indeed, as mentioned above, we have found Ocqueoc River water to extend as a surface plume 0.5 km offshore at nearly half of its original concentration. We find it interesting to speculate about how lacustrine lamprey might use odor cues to locate specific rivers. It is improbable that migrants are actively swimming back and forth between rivers and then selecting the stronger smelling one, the scenario tested here. Rather, it seems more likely that lamprey are attracted by the odor of the first river plume encountered. The probability of encountering a river plume might be influenced by several factors including search behavior, river discharge, plume structure, and odor concentration. In general, larger rivers tend to attract larger numbers of spawning lamprey (Morman et al. 1980), but after larvae are removed with lampricides, even large rivers attract very few adults (Moore and Schleen 1980). Our data support an interaction of odor and discharge: although the Cheboygan River has nearly eight times the flow of the Ocqueoc River, in 1997 its traps caught only twice the total number of lamprey (Schleen et al. 1998), a number which makes sense if one considers that Ocqueoc River water was the more attractive of the two when tested in our maze in 1997.

In conclusion, this study demonstrates that the odor of natural stream water is innately attractive to migratory sea lamprey when tested in a realistic fashion. Further, this study demonstrates that larval odor is a key component of river odor and that bile acids comprise a significant component of the pheromone. However, other components exist in both the pheromone and stream waters which appear to synergize each other's activity. Although notable, we recognize that our results were obtained in a controlled setting far removed from the scale of the Great Lakes. Clearly, a field experiment is needed to assess the potency of this pheromone to free-ranging lamprey and to determine whether and how it might be used in lamprey control.

Acknowledgements

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Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling

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Abstract: Minisatellite-based DNA profiling was used to investigate the dispersion of synchronously spawned families of Atlantic salmon (*Salmo salar* L.) fry from artificial nests in a natural stream. By the end of the summer, i.e., 17 weeks after hatching, detected dispersion was mainly downstream and less than 1 km. Within this distance, three families that had been stocked together showed different patterns of dispersion, with the relative abundance of each family changing systematically with distance downstream from the nest, but with no monopolization of any area or habitat type by any one family. The length of fry also changed systematically with distance downstream, with the patterns of change depending on family. For each family, fry were larger closer to the nest. Changes in habitat type had a common effect on the density and length of fry from all the families.

Résumé : La détermination des profils d'ADN microsatellite a permis d'étudier la dispersion de familles d'alevins du Saumon de l'Atlantique (*Salmo salar* L.) provenant de fraies simultanées dans des nids artificiels d'un cours d'eau naturel. À la fin de l'été, i.e., 17 semaines après l'éclosion, la dispersion s'observait surtout vers l'aval sur une distance de moins de 1 km. Sur cette distance, les trois familles qui avaient été ensemencées ensemble avaient des patterns de dispersion différents et l'importance relative de chaque famille changeait de façon systématique avec la distance en aval du nid, sans qu'aucune des familles ne monopolisât une section ou un habitat particuliers. La longueur des alevins variait aussi systématiquement avec la distance vers l'aval, chaque famille selon un agencement particulier, les alevins de chaque famille étant plus gros près du nid. Les changements de type d'habitat avaient le même effet sur la densité et la longueur des alevins de toutes les familles.

[Traduit par la Rédaction]

Introduction

Many stream-dwelling salmonids occur under conditions of low productivity and high competition, and survival has been shown to depend on cohort density (Elliott 1984). Considerable research effort has been focused on controls on cohort dynamics and those factors that affect overall population abundance. More recently, there has been increasing interest in the role of family-specific influences on survival. Variation in distribution, growth, and survival among families of young salmonids within streams may be important sources of differences in the relative performance of family groups, and perhaps a key factor influencing the performance of populations and the fisheries that exploit them (Geiger et al. 1997). Only recently have new DNA techniques made the identification of families in the field possible (Gross and Kapuscinski 1997; Carlsson et al. 1999; Fontaine and Dodson 1999).

Adult Atlantic salmon (*Salmo salar* L.) spawn in the autumn and winter months, constructing discrete spawning nests in stream gravels, which as aggregates form redds (Taggart et al. 2001). Areas of preferred spawning habitat are often patchily distributed and this results in locally high levels of egg deposition (Moir et al. 1998). Spawning activity therefore imposes spatial structuring on the initial distribution of progeny. Salmon fry emerge and disperse during the spring following spawning. Patterns of dispersal and survival are highly variable (Godin 1982; Gustafson-Greenwood and Moring 1990), and are affected by such factors as emergence timing (Crisp 1995; Einum and Fleming 2000), stream flow (Crisp 1995; Jensen and Johnsen 1999), and habitat type and quality (Heggenes and Borgstrøm 1991). Soon after emergence, fry set up and defend territories (Kalleberg 1958; Crisp and Hurley 1991), but initial dispersal across patches of suitable habitat increases the overall uptake of available territory space (Crisp 1995). Density-dependent interactions are most intense during this early period (Elliott 1984, 1986; Einum and Fleming 2000). In particular, fry emerging from composite or closely spaced redds compete at both the inter- and intra-family levels. Competition and dispersal are ex-

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pected to have profound effects on the dynamics of populations and their constituent family groups (Begon et al. 1990).

This paper describes a study in which family-specific DNA profiling was used to identify members of different families of salmon fry that had dispersed in natural stream habitat over the period preceding the end of their first summer. The main objectives were to (*i*) determine the patterns of dispersion and settlement for different family groups of fry from known point sources, (*ii*) establish whether the patterns were equivalent, and (*iii*) compare the sizes of fry from family groups in relation to habitat type and dispersal distance.

Materials and methods

The study site

The study site was a 2.3-km section of the Baddoch Burn, a small (second-order) spawning tributary on the upper reaches of the Aberdeenshire Dee in Northeast Scotland (Fig. 1). The stream rises to an altitude of 675 m and flows approximately eastwards for 8.25 km to join the Clunie at an altitude of 415 m. It drains an area of ca. 25 km^2.

The stream is shallow and fast flowing with some falls and deeper pools. It supports a wild, self-sustaining population of Atlantic salmon. Resident and migratory brown trout (*Salmo trutta* L.) also spawn in the stream's lower reaches. All adult fish ascending to the stream were captured by means of a trap. A study reach was established ca. 2 km above a natural cataract that effectively determines the upstream limit of natural spawning for salmon (Fig. 1). The study reach was 514 m long, had an average width of 5.8 m (range 2.9–9.2 m) and a mean gradient of 6%. It consisted of a linear patchwork of habitats defined by a range of local geomorphic and morphological influences.

Habitats were visually classified using Rosgen's methodologies (1996). Seven broad classes of habitat were designated types A, Ai, B, C, D, E, and F (see Table 1). Sectors of continuous habitat varied from 4 m to 25.8 m of stream length. The upper and lower limits of each sector were defined by breaks in local channel slope corresponding to small cascades and waterfalls or pools. A series of 16 sectors were defined as the main study reach. Three additional sectors (17–19) were established downstream of the main study reach (Fig. 1). Summary details of each sector are given in Table 2.

Construction of family groups

Between 1 October and 11 November 1993, 63 adult salmon (36 males and 27 females) were captured in the fish trap. An adipose fin clip from each fish was preserved in ethanol and stored under refrigeration (2°C) for DNA profiling. All adults were held for stripping or release until 11 November, when 11 males and 11 females were selected at random. Family groups of eggs were produced from single pair matings. Remaining fish were released to spawn naturally within the stream.

Egg incubation and planting

Family groups of eggs were incubated in a "Kashmir" type incubation system (Seymour 1970) constructed within one of the holding chambers of the fish trap. After eyeing (in early March), groups of 3000 eggs were counted for each family. Release baskets containing eyed eggs were placed in stream gravel on 12 March at five locations spaced at 500- to 675-m intervals in an array corresponding to a 3:1:3:1:3 family distribution (Fig. 1). In particular, family 4 was placed 460 m upstream of the study reach, families 5, 6, and 7 were placed 2.9 m upstream from the lower limit of sector 2, and family 8 was placed 27 m downstream of the lower limit of the main study reach. Each basket (20 cm × 20 cm) was lined with 2-mm-aperture plastic mesh to retain eggs but allow alevins and fry to escape. Those baskets containing three families had a separate compartment for each family to allow the estimation of prehatch survival within families.

Determination of egg size, hatch timing, and survival

For each family, hardened egg diameters were estimated by the method of Thorpe et al. (1984). Hatch date was determined for samples of eggs (ca. 50–80) from each family held within the stream in transparent perforated containers lined with 1-mm plastic mesh. Alevins were counted and removed every one to four days until the first week of June, when the number of dead or unfertilized eggs remaining in the release containers was counted.

Fry sampling procedure

All 19 sectors were electrofished between 29 August and 13 September, about 17 weeks after hatch. Fish were caught using a backpack apparatus (WFC.8 Smooth DC model, Electrocatch Ltd., Wolverhampton, England) and hand nets. Three consecutive fishings were carried out within each sector. All capture procedures were carried out while working upstream. To reduce fright bias and movement, electrofishing was restricted to areas of less than 300-mm depth, and sectors were isolated by stop nets where natural barriers did not exist. Electrofishing carried out over a 14-m section immediately upstream of sector 1 yielded only one 0+ fry.

All the fish obtained from each fishing were retained separately. Individuals were measured for fork length to the nearest millimetre after sacrifice (tricaine methanesulfonate, MS 222, Sandoz Laboratories; 1:10 000). Scales were taken from a subsample of fish to confirm age. A sample of dorsal muscle was obtained from each individual and stored in ethanol under refrigeration (2°C) prior to DNA extraction.

Parentage identification

Individual progeny were identified to family by genetic profiling of multiple minisatellite loci. DNA was extracted from ethanol-preserved tissue using a simplified methodology based on the use of phenol–chloroform (Taggart et al. 1992). Single-locus profiling was carried out as described by Taggart et al. (1995), employing an isotopic (^{32}P)-based protocol. A composite DNA size reference ladder, with 23 approximately evenly spaced bands in the range 1.8–12.1 kb, was included in each lane (Taggart and Ferguson 1994). This aided later scoring of bands (alleles) by direct visual inspection of autoradiographs.

The 22 parental fish whose progeny were used in the study were genotyped at nine polymorphic loci, for which between 4 and16 alleles segregated. A computer program that predicts the resolving power of various combinations of loci for identifying progeny where parental genotypes are known (Family Assignment Program, FAP; J.B. Taggart, unpublished data) was used to select the optimal loci for progeny screening. A combination of three loci (*Ssa-A10*, *Str-A9*, and *Str-A22/1*) provided potential 98.5% discrimination of progeny to family. Addition of a fourth locus (either *Ssa-A11* or *Ssa-A60*) resulted in potential 100% discrimination. All five loci were scored to provide a check for genotyping errors (caused by visual mistyping, allele mutation, or non-Mendelian segregation). Screening of five loci also provided a check for the unlikely, but possible, presence of progeny from naturally spawned fish within the experimental site. Simulations using FAP indicated that the five selected loci provided on average >98% discrimination between the 11 experimental families and all other possible families derived from the 51 wild spawners within the tributary. No anomalous progeny genotypes were recorded; therefore, a high degree of confidence could be placed in the detected family assignment outcomes. A second designed function of FAP was used to assign individuals to families according to their composite genotype.

Fig. 1. The study site in the Baddoch Burn, Northeast Scotland. Egg planting positions (F*) and sectors sampled during the study are shown.

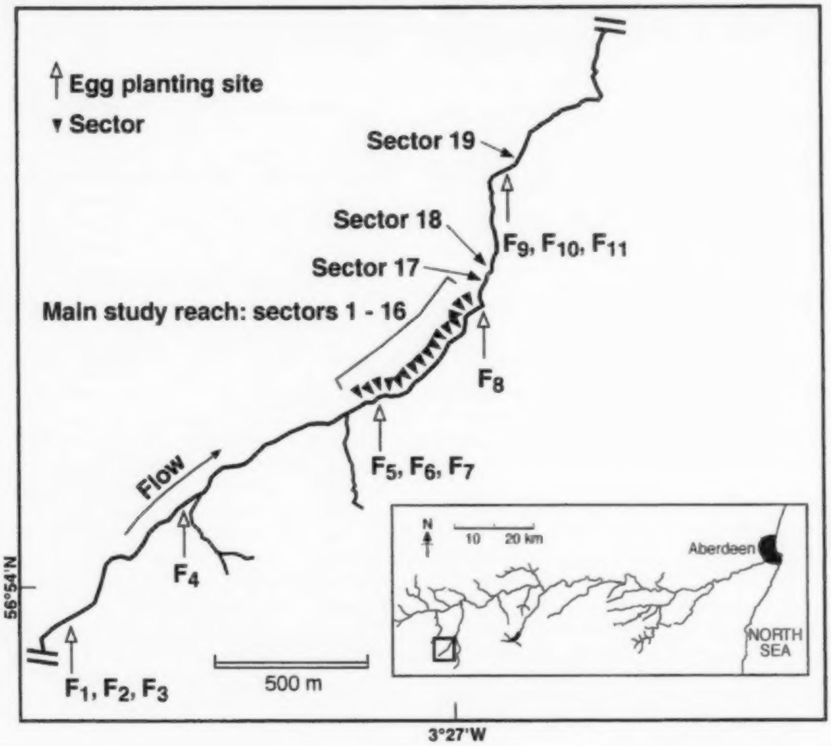


Table 1. Habitat classes and characteristics found in the main study reach.

Class	Description
A	Areas of broad channel of low gradient (<0.2%) with a high width–depth ratio (>12): bed materials dominated by scattered boulders with lesser amounts of cobble, gravel, and sand. Riffle habitat.
Ai	As above, but with the bed formed of unstable alluvial bar deposits of cobble and gravel.
B	Areas of moderately entrenched channel characterized by a series of rapids and narrow riffles and irregular spaced scour pools; channel containing predominantly boulders and cobble material.
C	Areas of steep and extensive rapids, characterized by irregular spaced pools and runs defined by bedrock features with many large boulders and some cobble material.
D	Areas of steep, high-energy, deeply entrenched, and confined stream channel containing predominantly boulder-sized material with some large (>50 cm) plunge pools.
E	Small (<2 m) waterfalls and cascades caused by local bedrock features or stabilized accumulation of slide debris and rockfall.
F	Pool habitat (>0.5-m depth) with an exposed bedrock base.

Statistics

Density and distribution of fry

The numbers of fry from each family caught in the main study reach (sectors 1–16) were modelled using generalized additive models (GAMs). GAMs are a flexible class of regression models that relate the response variable to arbitrary smooth functions of the explanatory variables. In particular, the shapes of the smooth relationships are determined, to a large extent, by the data themselves. GAMs therefore provide an attractive framework for modelling the dispersion of fry as a smooth function of distance downstream from a stocking point. Technical details of GAMs are described by Hastie and Tibshirani (1990). Examples of GAMs in the fisheries literature include Swartzman et al. (1994), Borchers et al. (1997), and Stratoudakis et al. (1998).

The basic formulation of the model follows the standard approach for "count" data (e.g., McCullagh and Nelder 1989). Specifically, let y_{fs} denote the number of fry from family f caught in sector s, $f = 1,\ldots,F$, $s = 1,\ldots,S$, and assume that y_{fs} is Poisson distributed with mean μ_{fs}. The parameter μ_{fs} is interpreted as the expected abundance of family f in sector s. In practice, however, changes in density are more interpretable than changes in abundance, and this is accommodated by writing

$$\mu_{fs} = \lambda_{fs} A_s$$

where λ_{fs} is the expected density of family f in sector s and A_s is the area of sector s. Transforming to the log scale gives

$$\log \mu_{fs} = \log \lambda_{fs} + \log A_s$$

The problem now is to relate log abundance or, equivalently, log density to explanatory variables such as habitat type or distance

Table 2. Sector characteristics, details of egg stocking locations, and the numbers of fry from each family caught in each sector.

Sector	Habitat	Midpoint distance (m)	Sector length (m)	Area (m^2)	Total catch (*n*)	Family								Stocking position
						F4	F5	F6	F7	F8	F9	F10	F11	
		−1310												F1[a], F2[a], F3[a]
		−560												F4
1[b]	C	−93	13.9	102	10	9	0	0	1	0	0	0	0	
2	B	−10	25.8	95	40	7	19	2	12	0	0	0	0	
		0*												F5, F6, F7
3	A	27	14.2	70	75	12	29	8	26	0	0	0	0	
4	B	39	9.8	40	32	0	8	4	20	0	0	0	0	
5	B	55	9.3	41	53	2	20	4	27	0	0	0	0	
6	B	71	14.5	62	56	2	12	11	31	0	0	0	0	
7	C	101	24.5	97	31	0	4	9	18	0	0	0	0	
8	D	125	18.4	72	18	0	6	5	7	0	0	0	0	
9	D	168	6	30	7	0	1	1	5	0	0	0	0	
10	C	181	8.4	58	34	2	4	9	19	0	0	0	0	
11	B	231	4	44	46	4	4	12	26	0	0	0	0	
12	A	264	10.8	64	65	3	17	14	31	0	0	0	0	
13	A	302	5.1	42	60	1	20	9	30	0	0	0	0	
14	Ai	353	14	80	50	3	12	20	15	0	0	0	0	
15	B	372	13.9	75	83	0	29	22	32	0	0	0	0	
16[c]	B	389	14.1	69	70	2	18	19	31	0	0	0	0	
		423												F8
17	B	458	4.9	54	59	0	5	9	5	40	0	0	0	
18	B	521	7.9	83	72	0	6	9	8	49	0	0	0	
		1261												F9, F10, F11
19	B	1352	5.2	58	48	0	0	0	0	0	22	15	11	

Note: Midpoint distance refers to midpoint distance (m) downstream from datum point.

[a] No individuals were detected in samples removed from sectors 1 to 19 (inclusive).

[b] Upper limit of main study area.

[c] Lower limit of main study area.

*Datum point.

downstream from a stocking point. Formally, this is done by modelling the counts y_{fs} assuming Poisson errors, a log link, and using log area as an offset variable (McCullagh and Nelder 1989).

Four explanatory variables were considered: (*i*) sector, a categorical variable with S levels, one for each sector in the main study reach; (*ii*) habitat, a categorical variable with 5 levels corresponding to habitats A, Ai, B, C, and D; (*iii*) distance downstream, a continuous variable that allows log density to vary either linearly or smoothly with the distance from the stocking point; and (*iv*) family, a categorical variable with F levels, one for each family. Sector, habitat, and distance downstream are related since they are all measures of location. Sector is the most general, but also the least interpretable. Habitat and distance downstream are more structured measures of location, and thus have the potential to provide more interpretable models.

First, a "full", or saturated, model was fitted to the data. This model has a separate parameter for each combination of family and sector, corresponding to a family main effect, a sector main effect, and an interaction between the two. A convenient way of expressing this model is

$$\text{log density} \sim \text{family} \times \text{sector}$$

where the × indicates the presence of both main effects and interactions. The model has too many parameters to be biologically useful, but provides a sensible benchmark for model comparison. Simpler models were then sought by a backwards-stepwise procedure. For example, the full model was first compared to

$$\text{log density} \sim \text{family} + \text{sector}$$

in which the interaction between family and sector is dropped, and

$$\text{log density} \sim \text{family} \\ \times (\text{habitat} + \text{smooth(distance downstream)})$$

in which sector is replaced by the combined effect of habitat and a smooth function of distance downstream. The interaction in the latter model allows for a family-specific relationship with both habitat and distance downstream; in particular, a separate smooth function of distance downstream is fitted for each family. Subsequent steps involved dropping interactions and main effects and replacing the smooth function of distance downstream with a linear function and no relationship at all.

Model selection was based on Akaike's Information Criterion (AIC) defined as

$$\text{AIC} = \text{model deviance} \\ + (2 \times \text{number of model parameters})$$

AIC penalizes models with many parameters and tends to lead to relatively simple models, particularly when categorical explanatory variables are involved. The best model was taken to be the model with fewest parameters within 2 units of the minimum AIC (Jones 1993). The adequacy of the final model was also assessed by residual plots.

Fry length

A similar procedure was used to model the length of fry from each family caught in the study reach. The lengths of fry from family f in sector s were assumed to be normally distributed with expectation μ_{fs} and constant variance σ^2. A full model was first fitted to the data, again with a separate parameter for each combination of family and sector, and simpler models were then investigated. AIC is now given by

$$\text{AIC} = (\text{model deviance}/s^2) + (2 \times \text{number of model parameters})$$

where s^2 is an estimate of σ^2 obtained from the full model.

Results

Egg size, hatch timing, and survival

Egg size varied between families. Mean diameter ranged from 4.60 mm in family 4 to 6.40 mm in family 5. The mean diameter of eggs from families 6 and 7 were 5.70 and 5.75 mm, respectively.

Hatching took place from 4 to 11 May. Hatch duration varied between families, lasting for between 5 and 7 days. Time of hatch did not differ between families (Kruskal–Wallis test, $p = 0.905$). Survival to hatch exceeded 98% for all 11 families.

Distribution and density of fry

Salmon fry were captured in all stream sectors. No genetic mutations and no evidence of non-Mendelian segregation of alleles were detected among the fry genotypes. Using composite genotypes, all fry could be unambiguously assigned to one of the 11 experimental families. No fry from adults released to spawn below the study reach were detected. Larger, older salmon parr (mean fork length 120.5 mm; range 93.5–151 mm) from stocking carried out before 1994 were captured in all but sector 6 (mean density 1.8 individuals·sector^{-1}; range 1–3). Native brown trout were caught in all sectors.

The fry population in the main study reach (sectors 1–16) was dominated by families 5, 6, and 7, which had been stocked at the lower end of sector 2. Some fry from family 4, stocked 460 m upstream of the study reach, were also present. No fry from the families stocked 1210 m upstream of the study reach, or from any of the families stocked downstream of the study reach were detected. Fry in sectors 17 and 18 were dominated by family 8, which had been stocked 32 m upstream of sector 17, but a few fry from families 5, 6, and 7 were also present. Only fry from families 9, 10, and 11 were found in sector 19. No fry was caught more than 940 m downstream or 90 m upstream from its stocking point.

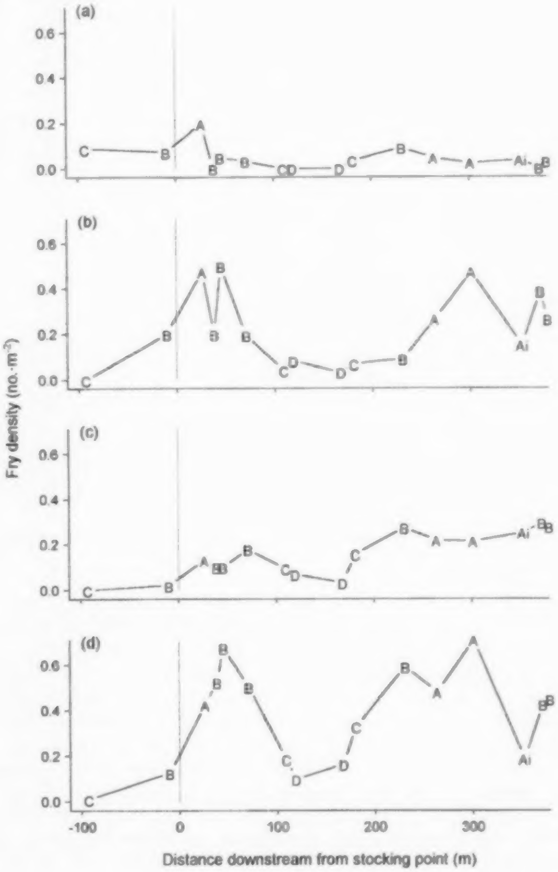
Figure 2 shows the densities of families 4, 5, 6, and 7 in each sector of the main study reach. The plotting symbol denotes the corresponding habitat type. There were clear differences in fry densities between families. Densities were generally lower in habitats C and D. Two important features of the data concern the numbers of fry close to the stocking point in sector 2 (see also Table 1). Only one fry from families 5 to 7 was caught in sector 1, about 93 m upstream of the stocking point. Equally, the numbers of family 4 showed a marked decline downstream of the stocking point for families 5 to 7, with 28 fry caught in sectors 1 to 3, but only 19 fry caught in sectors 4 to 16.

Modelling of fry density was restricted to families 5, 6, and 7 to focus on the dispersion of fry from different families from the same stocking point. A simple model of fry density could only be found when analysis was further restricted to the data obtained downstream of the stocking point (i.e., sectors 3–16). Density could then be adequately modelled as

$$\text{log density} \sim \text{habitat} + \text{family} \times \text{smooth(distance downstream)}$$

The first term indicates that habitat had a significant effect on density ($p < 0.0001$). Further, there was no evidence of an interaction between family and habitat, so changes in habitat affected the densities of the three families in the same way. The second term indicates that density depended on family and distance downstream ($p < 0.0001$ in both cases). Further, the relationship with distance downstream was smooth and nonlinear (on the log scale), and a different relationship was required for each family ($p < 0.0001$) (i.e., there was an interaction between family and distance downstream). Thus, the three families showed different patterns of dispersal, with the relative abundance of each family chang-

Fig. 2. The densities of families (*a*) 4, (*b*) 5, (*c*) 6, and (*d*) 7 in each sector of the main study reach. Family 4 was stocked 460 m upstream of the study reach. Families 5, 6, and 7 were stocked at the datum point (0). The plotting symbol denotes the habitat type of each sector. The horizontal axis shows the distance of the midpoint of each sector downstream from the stocking position. The thin vertical line emphasizes the position of the stocking point.



ing systematically with distance downstream. Three degrees of freedom were used to model each smooth relationship (Hastie and Tibshirani 1990), roughly equivalent to fitting a cubic. Residual plots confirmed that the model was an adequate description of the data, and that the assumption of Poisson errors was reasonable.

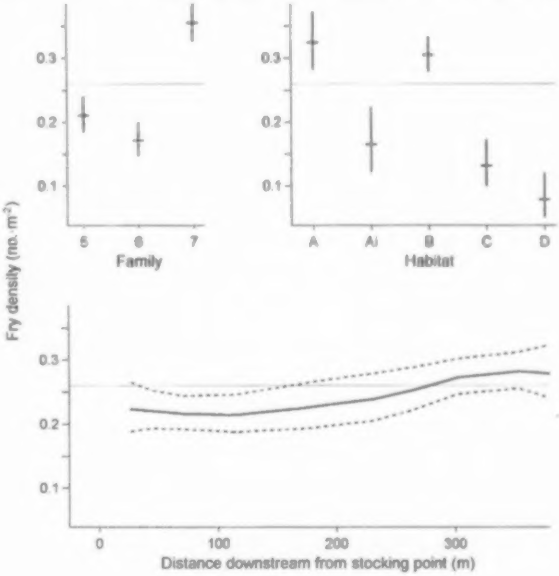
The fitted model is most easily interpreted graphically. Figure 3 shows the effect of habitat and the main effects of family and distance downstream, with approximate pointwise 95% confidence intervals. The effects were estimated on the log scale, but have been back-transformed to the original density scale for presentation. They have also been centred around an estimate of mean density, indicated by the thin horizontal line. The habitat effect shows that densities in habitats Ai, C, and D were lower than in habitats A and B. However, since there was only one sector with habitat Ai, the result for this habitat should be treated with caution. The family main effect shows how density depends on family, averaged across sectors 3 to 16. Thus, family 7 was more abundant, on average, than both families 5 and 6. Similarly, the main effect of distance downstream shows how density depends on distance downstream averaged across the three families (and having adjusted for the effect of habitat). Thus, on average, density increased slightly with distance downstream from the stocking point. However, this main effect of distance downstream excludes the fry from family 4, and when these were included, average density was relatively constant throughout sectors 3 to 16.

The main effects of family and distance downstream are useful summary measures, but the interaction term contains the most important information about the relationship between density, family, and distance downstream. Figure 4 shows the interaction by plotting the fitted relationship between density and distance downstream for each family. The broken lines are approximate pointwise 95% confidence intervals on each fitted relationship. The density of family 7, the most abundant family, was relatively constant throughout the study reach (adjusted for the effect of habitat). In contrast, the density of family 6 increased with distance downstream, whilst the density of family 5 first decreased and then increased again. By sector 16, the furthest point downstream in the study reach, the densities of families 5, 6, and 7 were comparable. Fry from families 5, 6, and 7 were found in roughly equal numbers in both sectors 17 and 18, consistent with their relative abundance in sector 16.

Some caution is needed when interpreting models of this type in case the effects of habitat and distance downstream are confounded. For example, if all of the poorest habitat was furthest downstream and fry density was low in this area, then it would not be possible to determine whether the low fry density was due to poor habitat or to having reached the limit of fry dispersion. In this study however, the main region of low uptake was in the middle of the study area, with good uptake on either side, so it is probably valid to regard the smooth functions of distance downstream in Fig. 4 as patterns of dispersion away from the stocking point.

It was not possible to find a simple extension of the model to include the data from sectors 1 and 2 because the densities of families 5, 6, and 7 declined so rapidly immediately above the stocking point (even allowing for habitat type). In particular, the decline was so marked that it could not be captured by a smooth function of distance. The pattern of dispersal upstream was therefore very different to that downstream.

Fig. 3. The main effects of habitat, family, and distance downstream on fry density, with approximate pointwise 95% confidence intervals. The thin horizontal line is an estimate of mean density.



Fry length

Modelling of fry length in the main study area was again restricted to families 5, 6, and 7. The single fish caught in sector 1 was excluded, so the analysis was focused on fish caught in sectors 2 to 16. Fry length was adequately modelled by

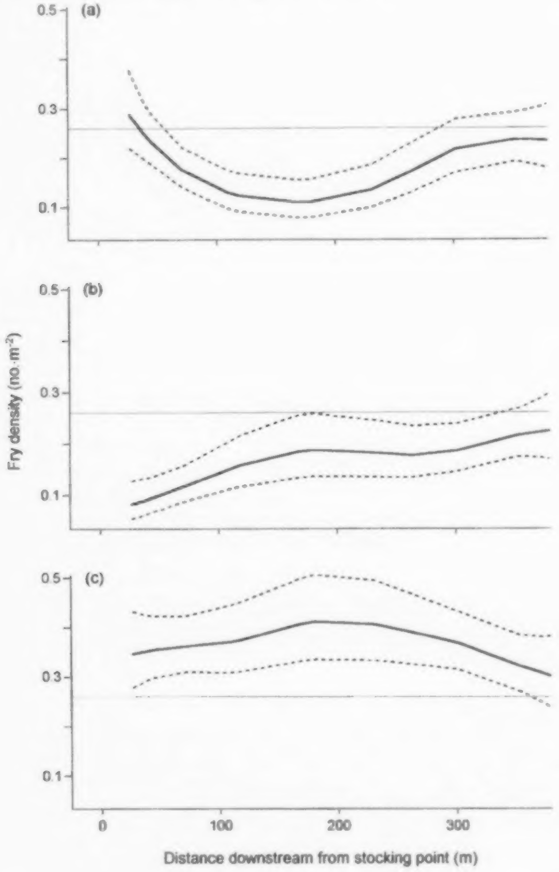
$$\text{length} \sim \text{habitat} + \text{family} \times \text{smooth(distance downstream)}$$

The effect of habitat and the main effects of family and distance downstream are shown in Fig. 5. The fitted relationships between length and distance downstream for each family are shown in Fig. 6.

Habitat had a significant effect on fry length ($p = 0.012$). Further, the effect was similar for all three families, since there was no evidence of an interaction between family and habitat. Fry in habitat D were smaller than in any of the other habitats, but there were no differences in fry length among the remaining habitats (Fig. 5).

Fry length also depended on family and distance downstream ($p < 0.0001$ in both cases). Again, the relationship with distance downstream was smooth and nonlinear, and a different relationship was required for each family ($p = 0.002$). Averaged over the study area, fry from family 7 were longer than fry from families 5 and 6 (Fig. 5). Further, averaged over families, fry were longest close to the stocking point (Fig. 5). The family-specific relationships between length and distance downstream (Fig. 6) show that fry from the three families were longest, and of comparable size, around the stocking point. Fry length then decreased with

Fig. 4. The fitted relationships between density and distance downstream, with approximate pointwise 95% confidence intervals (broken lines), for families (*a*) 5, (*b*) 6, and (*c*) 7. The thin horizontal line is an estimate of mean density.

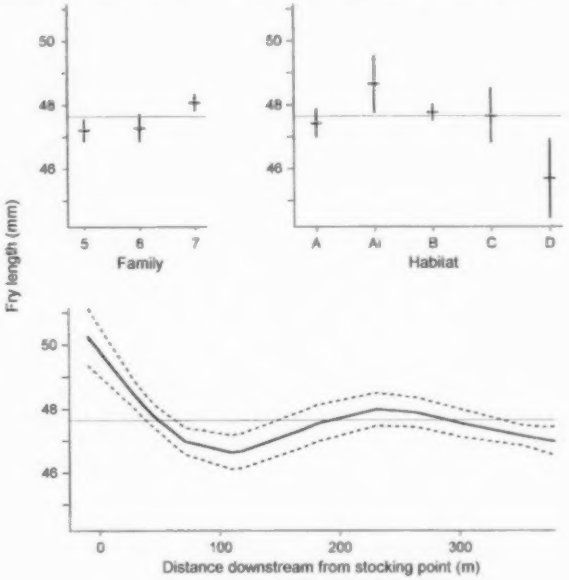


distance downstream, until about 100–150 m downstream. The lengths of fry from family 7, the most abundant family, decreased less than those from other families: i.e., fry from family 7 were bigger in this part of the study reach. From about 200 m downstream, there were no clear differences between the lengths of fry from different families. Four degrees of freedom were used to model the smooth relationships, which permits substantial flexibility in the shape of the fitted curves. However, similar conclusions were obtained if fewer degrees of freedom were used, and the findings therefore appear robust to the amount of smoothing. The lengths of the fry from families 5, 6, and 7 caught in sectors 17 and 18 were similar to the lengths observed in sector 16.

Discussion

The factors that influence the distribution of salmonid fry from redds are poorly understood (Heggenes 1990). Patterns of movement depend on such factors as physical habitat, water flows, densities, and the presence of other fish (Heggenes and Borgstrøm 1991; Beall et al. 1994). The present study has shown that family membership is also an effect and that variable patterns of family dispersion are accompanied with systematic variations in body length. Recently, egg size has been identified as an effect on posthatch performance (Einum and Fleming 2000). Only three families were examined in detail in the present study. Family 5 was notably larger at the egg stage than the others but this was not obviously associated with later differences in dispersion, body length, or relative abundance.

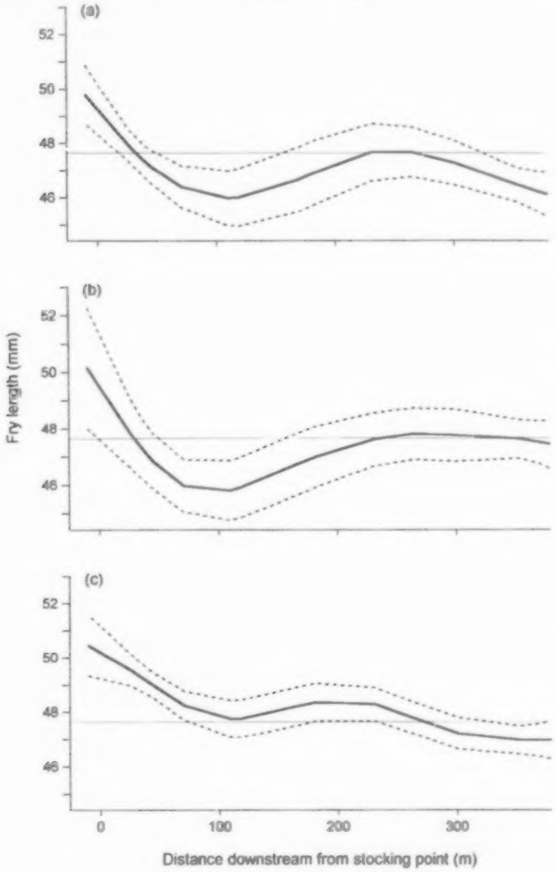
Fig. 5. The main effects of family, habitat, and distance downstream on fry length, with approximate pointwise 95% confidence intervals. The thin horizontal line is an estimate of mean length.



It was not possible to estimate the limits of dispersion. For the three families examined in detail, most progeny were located over a distance of 380 m downstream of the point source from which the fry emerged. Small numbers of fry were detected 520 m downstream of the stocking point, but none were detected 1350 m downstream. Distribution upstream of the stocking point was extremely curtailed. Furthermore, no fry were detected in the study reach that had been stocked more than ca. 1.5 km above its upper limit, or at any distance below its lower one. Detected dispersion was predominantly downstream and restricted to distances of <1 km. This is broadly consistent with the findings of studies carried out elsewhere in both natural and artificial stream channels (Egglishaw and Shackley 1973; Kennedy 1982; Crisp 1995).

The sectors surveyed were characterized by a range of microhabitats, which were likely to vary in suitability for salmon fry. Overall, fry numbers reflected this variation, with lower densities in habitats of types C and D. Fry were also smaller in habitat D, irrespective of family origin. These observations support the concepts of differential settlement according to habitat preference and according to differences in the carrying capacity of different habitat types (for review,

Fig. 6. The fitted relationships between length and distance downstream, with approximate pointwise 95% confidence intervals (broken lines), for families (*a*) 5, (*b*) 6, and (*c*) 7. The thin horizontal line is an estimate of mean length.



see Heggenes 1990), but may also reflect, in part, variations in sampling efficiency owing to local instream habitat conditions.

There were significant differences in the dispersion profiles of the three families examined, with their relative abundance changing systematically with distance downstream of the stocking point. Since there was no evidence of monopolization of particular areas or habitats by fry from any one family, relative distribution must be determined in some other way. Several authors have suggested that patterns of family distribution result from active, exploratory behaviour driven by competition (Fontaine and Dodson 1999). Social interactions were not recorded in this study and the dynamics of dispersal or mortality in the period before sampling were not examined. Ultimately, however, social factors regulate the behaviour of all territorial fish in streams (Chapman 1962; Fontaine and Dodson 1999) and interactions must occur at both the individual and family levels. Individual responses are probably dependent on many local social factors, including the presence of older individuals and population density (Heggenes and Borgstrøm 1991; Beall et al. 1994), predation pressure (Brännäs 1995), and the presence of kin (Brown and Brown 1993).

In addition, the first individuals to emerge from redds may obtain the best habitat (Brännäs 1995), resulting in faster growth and lower mortality than for those emerging and dispersing later (Chandler and Bjornn 1988; Einum and Fleming 2000). Within family groups, early emerging individuals tend to be dominant over later emerging ones, perhaps as a result of intrinsic metabolic differences. Later-emerging fry may therefore be displaced to suboptimal habitat by the dominance of competitors that have emerged earlier and have prior residence (O'Connor et al. 2000). Thus, for fully stocked streams, survival and growth rates may be lower among fish forced by competition to move further away from their site of emergence (Elliott 1986; Titus and Mosegaard 1991). The observed variations in body size within families with distance downstream may reflect these types of effects.

The distribution of spawning habitat in spawning streams is nonuniform. As a result, eggs are distributed nonuniformly through potential fry-rearing habitat (Moir et al. 1988). Density-dependent mortality rates are especially high in the posthatch phase (Einum and Fleming 2000) and selective pressure is expected to favour mechanisms promoting active dispersal before settlement. In general, the extra costs of greater dispersal are expected to be offset by a greater than average probability of locating vacant territory of higher quality. The fittest progeny may be those that display either a greater or less than average intrinsic tendency to disperse (Howard 1960). On the other hand, where spawning is patchy, more extensive dispersal is associated with a greater risk of contact with competitors derived from other redds. The curtailed edge of the lower limit for dispersal of family 4 suggests that substantial interactive effects occur in areas where fry showing a high tendency to disperse converge with fish that have remained near their point of emergence. In addition, natural spawning by Atlantic salmon generates complex, half-sib family groups (Hutchings and Myers 1988; Thomaz et al. 1997; Taggart et al. 2001). Kin relationships are a determinant of the relationships between individuals and their spatial distributions (Brown and Brown 1993). In the present study, the use of simplified family groups for genetic identification precluded the inclusion of half-sibs and their absence may have resulted in a more structured pattern of distribution than would normally be evident in the wild (Fontaine and Dodson 1999). Thus, where natural spawning occurs, complex family effects occurring on multiple scales for both active dispersion and competitive displacement are likely to affect the size and structure of the new cohort.

We have shown that the dispersion of a small number of synchronously spawned family groups of salmon fry through natural habitat at the end of their first summer is complex and nonrandom, even on very local scales. The observed patterns of dispersion broadly align with the concept of "dispersal structures" in streams as described by Downes and Keough (1998). Knowledge of the factors that influence the relationship between patterns of adult spawning and the distribution and performance of their progeny will aid management (e.g., in relation to stocking protocols) and investigation of stream populations of salmonids (e.g., by conditioning sampling strategies). Our study is among the first to use molecular genetic techniques in experimental field studies of salmonids and is therefore essentially descriptive. However, we have identified the scaling of dispersion by different family groups, and perhaps, identified some of the so-called unknown factors (see Heggenes 1990; Heggenes and Saltveit 1990; Heggenes and Borgstrøm 1991) that influence patterns of habitat uptake.

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Aluminum-dominated acute toxicity to the cladoceran *Ceriodaphnia dubia* in neutral waters downstream of an acid mine drainage discharge

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Abstract: Acid mine drainage (AMD) is traditionally considered to impact aquatic ecosystems by acidification, metal precipitation smothering stream substrates, and sediment toxicity in association with trace metals. Using *Ceriodaphnia dubia* as a test organism, we conducted whole effluent toxicity (WET) tests with both field-collected and laboratory-synthesized AMD samples to investigate possible mechanisms of reduced benthic macroinvertebrate community diversity in neutral (pH > 7.0) waters downstream of an acidified tributary. Our results indicate that Al and Fe in transition from acidic waters to neutralizing receiving streams can cause acute toxicity to standard invertebrate test organisms at neutral pH. Aluminum, with an average LC_{50} (50% lethal concentration) of 2880 $\mu g \cdot L^{-1}$, was determined to be the cause of acute toxicity in the field for up to a mile downstream of the AMD-influenced tributary and was the likely cause of reduced community diversity at those sites. Although Fe singly may cause acute toxicity in this type of system, it appears to reduce the toxicity of combinations of other metals such as Al, Cu, and Zn.

Résumé : Les rejets acides des opérations minières (AMD) affectent les écosystèmes aquatiques, croit-on, par l'acidification, la précipitation de métaux qui encrasse les substrats des cours d'eau et la toxicité des sédiments associée à la présence de métaux en traces. Nous avons utilisé *Ceriodaphnia dubia* comme organisme expérimental pour effectuer des tests de toxicité de l'effluent entier (WET) avec des échantillons d'AMD récoltés sur le terrain et d'autres synthétisés en laboratoire pour déterminer les mécanismes qui causent une réduction de la diversité de la communauté des macroinvertébrés dans des eaux neutres (pH > 7,0) en aval d'un tributaire acidifié. Nos résultats indiquent que l'Al et le Fe en transition depuis les eaux acides vers les cours d'eau récepteurs neutralisants peuvent causer une toxicité aiguë chez les organismes étalons à un pH neutre. L'aluminium, qui a une concentration létale LC_{50} moyenne de 2880 $\mu g \cdot L^{-1}$, s'avère être la cause de la toxicité aiguë qui s'observe sur le terrain jusqu'à 1 mille en aval d'un tributaire affecté par l'AMD et il est la cause probable de la réduction de la diversité de la communauté à ces sites. Bien que le Fe puisse causer une toxicité aiguë dans ce genre de système, il semble qu'il réduise la toxicité des combinaisons d'autres métaux tels que l'Al, le Cu et le Zn.

[Traduit par la Rédaction]

Introduction

A number of investigators have studied the toxic interactions of reduced pH and increased metal concentrations in aquatic systems, a scenario produced in the field by acid precipitation and acid mine drainage (AMD). AMD occurs when minerals containing reduced forms of sulfur (pyrites, sulfides) are oxidized upon exposure to water and oxygen. The oxidation process results in production of strong acids, which mobilize acid-soluble metals, including iron (Fe), aluminum (Al), copper (Cu), zinc (Zn), and others depending on the mineralogy of the disturbed area. The mixture of acid and dissolved metals creates a severe environment for aquatic organisms. Numerous studies have documented the impacts of AMD upon aquatic communities in acidified stream reaches (e.g., Roback and Richardson 1969; Armitage 1980; Kelly 1988); these impacts include reduced taxon richness and abundance and (or) a shift from pollution-sensitive to pollution-tolerant species.

Although the pH-related ecosystem impacts of AMD are well documented, AMD can also cause impairment to aquatic organisms beyond where surface waters are acidified. Sediment toxicity may occur where trace metal concentrations are high (Kemble et al. 1994). Ferric hydroxide precipitate (a product of pyrite oxidation) is thought to cause ecosystem impairment by smothering available habitat and reducing periphyton productivity (Scullion and Edwards 1980; McKnight and Feder 1984). Solid ferric hydroxide also has been shown to cause acute toxicity to *Daphnia magna* in the absence of dissolved Fe (Soucek et al. 2000*a*). Furthermore, Al has been observed to cause acute toxicity to fish in mixing zones (pH 4.8–6.5) below acidic tributaries (Rosseland et al. 1992; Henry et al. 1999; see also review by Gensemer and Playle 1999) and to alter snail behavior through ingestion (Elangoven et al. 1997; Campbell et al. 2000). These findings suggest that AMD is a complex pollutant that can impair aquatic ecosystems in a variety of

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ways, and that further research should include effects beyond the zone of pH depression.

We observed benthic macroinvertebrate community impairment within three circumneutral sites downstream of Lick Branch, an acidified tributary to Puckett's Creek of the Powell River watershed, southwestern Virginia, U.S.A. At these sites, several community indices, including total abundance, Ephemeroptera–Plecoptera–Trichoptera (EPT) richness, and percent Ephemeroptera abundance, were significantly lower than at stations upstream of AMD inputs or stations further downstream with additional dilution (Soucek et al. 2000*b*). These community impacts extended approximately 1 mile (~1.61 km) downstream of the confluence of the acidified tributary, but despite the observed precipitation of metals at these sites, sediment tests with standard test organisms did not detect toxicity. Therefore we hypothesized that impairment was due to water-column toxicity, and we conducted laboratory tests with both field-collected water samples and synthesized AMD effluents to determine the relative toxicity of various mixtures of four metals (Al, Fe, Cu, Zn) found in the discharge. Furthermore, we evaluated the role of metal precipitation or formation of metastable complexes in the toxic mechanism of the discharge. The cladoceran *Ceriodaphnia dubia* was chosen as the test organism as responses of this organism to AMD samples were previously observed to correlate significantly with several benthic macroinvertebrate community indices for this watershed (Soucek et al. 2000*b*).

Materials and methods

Experimental design

Investigation of the toxic mechanisms in the circumneutral pH sites began by collecting water samples from the discharge source in Lick Branch (designated as station LB-3) and from three points in the neutralizing receiving stream, Puckett's Creek (Fig. 1). Acute toxicity tests were conducted with these samples using *C. dubia* to obtain 48-h LC_{50} (50% lethal concentration) values and (or) percent survival in full-strength samples. Then, metals analyses were conducted on the samples to determine Al, Cu, Fe, and Zn concentrations in addition to pH and conductivity values.

Next, a number of artificial AMD effluents were formulated in the laboratory containing acid alone or acid plus one to four metals in various combinations at pH, conductivity, and metal concentrations similar to those measured for the AMD discharge. These artificial effluents were used as starting solutions in whole effluent toxicity (WET) tests with a 50% dilution series mimicking downstream dilution. Then, mean LC_{50} values were calculated for each artificial effluent, and metal concentrations at LC_{50} values were calculated based on measured metal concentrations in starting solutions. Comparison of metal concentrations at LC_{50} values for artificial effluents with those in field-collected samples from the LB-3 discharge and the three downstream stations allowed determination of which metals had the largest toxic role in the neutral receiving stream. Then, Marking's additive index (MAI, Marking 1977) values were calculated to determine if metal combinations acted synergistically or antagonistically. In addition, the hypothesis that precipitation of Al and Fe or formation of metastable complexes was involved in the mechanism of AMD toxicity was tested by conducting time-delayed toxicity assays.

Water chemistry of field-collected AMD samples

Water samples were collected from the LB-3 discharge in Lick Branch, a tributary to Puckett's Creek, Powell River drainage, southwestern Virginia, U.S.A., and from three stations in Puckett's Creek downstream of Lick Branch (Fig. 1). The three Puckett's Creek stations were immediately downstream (station PC-4), 0.5 miles downstream (PC-2), and 1 mile downstream (PC-1) of Lick Branch. To obtain background water chemistry data for the receiving system, one site upstream of the discharge in Lick Branch (LB-4) and one site upstream of the acidic tributary in Puckett's Creek (PC-5) were sampled. Samples were stored at 4°C until analyzed.

Water-quality parameters including pH, conductivity, and dissolved oxygen were measured for each sample, and alkalinity, acidity, and hardness were measured where appropriate. The pH was measured using an Accumet® (Fisher Scientific, Pittsburgh, Pa.) pH meter equipped with an Accumet® gel-filled combination electrode (accuracy $< \pm 0.05$ pH at 25°C). A Yellow Springs (RDP, Dayton, Ohio) model 54A meter was used to measure dissolved oxygen. Conductivity measurements were made using a Hach® (Hach, Loveland, Colo.) conductivity/TDS meter. Alkalinity, acidity, and hardness were measured by titration as described in APHA et al. (1995). In addition, water-column samples were analyzed for total Al, Cu, Fe, and Zn concentrations. Cu and Zn were previously determined to be the most concentrated trace metals in the discharge (D.J. Soucek, unpublished data). Samples were acidified, filtered (0.45 μm pore size), and then analyzed by inductively coupled plasma spectrometry. Lower detection limits for metals were 1 (Al), 0.5 to 1.8 (Cu), 2 (Fe), and 2 $\mu g \cdot L^{-1}$ (Zn).

Culturing of test organisms

Ceriodaphnia dubia were used in toxicity tests and were cultured in filtered water from a nontoxic reference stream near Newport, Virginia (Sinking Creek). Analysis of the culture water indicated that metal concentrations were low to undetectable (2 $\mu g \cdot L^{-1}$ Al, 14 $\mu g \cdot L^{-1}$ Fe, and Cu and Zn were below detection limits). Average (± standard deviation, SD) pH, conductivity, alkalinity, and hardness for culture water were 8.0 ± 0.1, 225 ± 5 μS, 131 ± 9 $mg \cdot L^{-1}$ as $CaCO_3$, and 123 ± 4 $mg \cdot L^{-1}$ as $CaCO_3$, respectively. Before testing, organisms were fed a diet of *Selenastrum capricornutum* and a YCT (yeast – cereal leaves – trout chow) mixture daily at a rate of 0.18 mL each per 30 mL water.

Water-column toxicity testing with field-collected samples

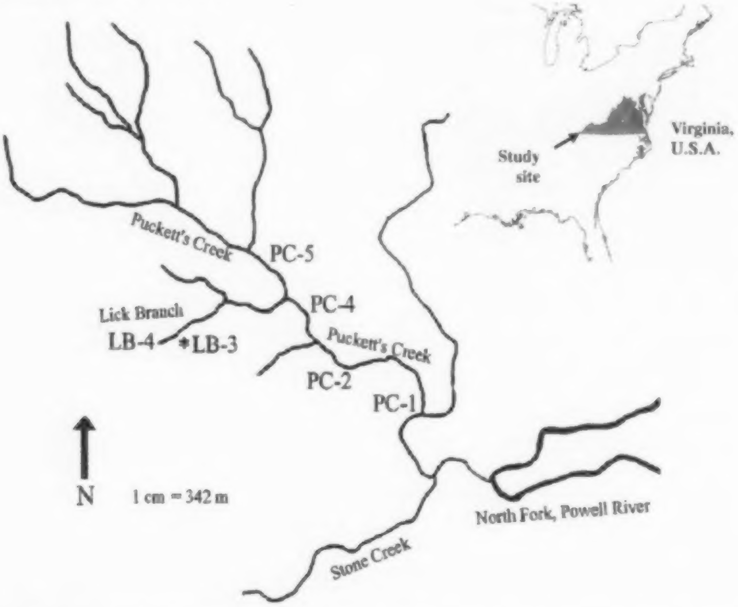
Seven replicate whole-effluent toxicity tests were conducted with the LB-3 discharge effluent sample according to U.S. Environmental Protection Agency (EPA) methods (U.S. EPA 1993). U.S. EPA (1993) "moderately hard synthetic freshwater" was used to dilute the effluent (50% dilution series) and as a control. The lowest concentration used was 0.78%. Five organisms were placed into each of four replicate 50-mL beakers per concentration for 48 h. Tests were conducted at 25°C. At the end of the test period, the number surviving per concentration was recorded, and LC_{50} values were calculated using the Spearman–Karber method.

For the three downstream stations (PC-1, PC-2, and PC-4), only undiluted samples were tested. Samples from these sites were collected, analyzed for water chemistry parameters as described previously, and tested for toxicity on two separate occasions: under moderate- and low-flow conditions. Again, four replicate beakers were used per site, with five organisms per 50-mL beaker. Percent survival for each station was recorded after 48 h.

Synthetic AMD solutions

After water chemistry data for the LB-3 discharge were collected, synthetic AMD solutions were made to simulate the field-collected sample. The first synthetic AMD effluent, containing all four measured metals, was designated S-LB-3 (synthetic LB-3). Metal salts (Al, Cu, Fe^{3+}, and Zn sulfates) were added in appropriate concentrations to moderately hard synthetic freshwater acidified to a pH of approximately 2.7 with sulfuric acid. With metal salts added to the acidic solution to ensure complete dissolution,

Fig. 1. Map of study area indicating study sites in Virginia, U.S.A. LB-3 was the acid mine drainage discharge, and PC-4, PC-2, and PC-1 were downstream stations with neutral pH values. LB-4 and PC-5 were stations analyzed for background water chemistry data. Approximate latitude and longitude: 36.7°, – 83.2°.



the pH, conductivity, and acidity then were adjusted to appropriate levels using sodium bicarbonate and sulfuric acid.

Nine other synthetic solutions also were developed to investigate individual and interacting effects of metal combinations and acid. They contained zero to three of the four metals at concentrations equal to those present in the LB-3 sample and had the same pH, conductivity, and acidity. In addition to four solutions containing only one of the four metals, combinations of Al–Fe, Cu–Zn, Al–Cu–Zn, Cu–Zn–Fe, and acid only were synthesized. These solutions served as starting points for WET tests, diluted in a 50% series with moderately hard synthetic freshwater and conducted as described previously for the field-collected sample. Three to four WET tests were conducted with each starting solution to allow statistical comparison. The starting solutions then were analyzed for appropriate metal concentrations as described previously to confirm nominal concentrations. Mean LC_{50} values for synthesized solutions and the LB-3 sample were compared by analysis of variance (ANOVA) using JMP IN ® software (Sall and Lehman 1996) to determine how well the synthesized solutions simulated the actual effluent. Student's *t* test was used for pairwise post-hoc analysis at the $\alpha = 0.05$ level.

Synergism and (or) antagonism in metal mixtures

To investigate possible synergistic and (or) antagonistic toxic effects of combinations of two, three, and four AMD metals, MAI (Marking 1977) values were calculated using the following formula:

$$(1) \qquad (Am/Ai) + (Bm/Bi) + (Cm/Ci) + (Dm/Di) = S$$

where A, B, C, and D are different metals, *i* is the LC_{50} of the metal individually, and *m* is the LC_{50} of the metal in the given mixture. The index value is made symmetric about zero as follows:

$$(2) \qquad \text{if } S \geq 1.0, \text{ MAI} = -S + 1.0$$

$$(3) \qquad \text{if } S \leq 1.0, \text{ MAI} = (1/S) - 1.0$$

If the MAI value is positive, then the mixture is synergistic, whereas negative values indicate antagonism. Statistical significance then can be inferred by inserting mean 95% confidence limits into the MAI equations. The lower limits of the individual concentrations (A*i*, B*i*, etc.) and the upper limits of the mixture concentrations (A*m*, B*m*, etc.) are used to determine lower limits of the index. Likewise, the upper limits of the individual concentrations and the lower limits of the mixture concentrations are used to calculate the upper limits of the index. This method provides the greatest deviation from the LC_{50} additive index. If upper and lower confidence limit MAI values do not overlap zero, the LC_{50} MAI value is considered different from zero (Marking 1977).

Precipitation experiments

Others have suggested that the mechanism of Al toxicity to fish is the process of hydroxide precipitation, forming polymers on fish gills upon neutralization (Poléo 1995; Exley et al. 1996; Gensemer and Playle 1999). Therefore, we conducted additional assays with both Fe and Al individually to test the hypothesis that precipitating metals played a role in the toxic mechanism of AMD in our system. We did this by placing test organisms into a neutralized solution containing Al or Fe immediately after mixing and at a given time period thereafter. We proposed that if the difference in organism survival in these different treatments was significantly greater than that explained by increased organism fitness on additional time spent feeding and growing, it may be concluded that the precipitation process is contributing to toxicity of the solution. That is, if organisms survive better in a solution after precipitation has occurred for a time, then the precipitation process may be the mechanism of toxicity.

Starting solutions were prepared as described previously with each metal at its appropriate concentration (as measured in LB-3) and at pH 2.9. Then, solutions with metal concentrations equal to the 48-h LC_{50} values (as determined in this study) were prepared by mixing starting solutions with appropriate amounts of moderately hard synthetic water (U.S. EPA 1993), causing neutralization of the solution. Each solution was poured into two sets of five beakers concurrently. Test organisms (*C. dubia*, five per beaker) then were placed into the beakers at time zero (immediately after mixing) and at 8 h after mixing (five replicates each). The 8-h time period was determined in preliminary experiments to be the point at which nominally increased survival was observed in tests with aluminum (D.J. Soucek, unpublished data). Nominal increases in survival were not observed within the first 0.5 to 4 h in preliminary experiments. The pH was measured in each set of beakers upon addition of test organisms, and metal concentrations were measured as described previously. Percent survival was determined for each solution 48 h after organisms were added.

To ensure that changes in mortality over time were not due to increased age or fitness of test organisms, the same tests were conducted with sodium chloride (2.5 $g{\cdot}L^{-1}$ NaCl). This salt should remain dissolved indefinitely under the test conditions used; thus, any decrease in mortality during the salt tests should be due to increased fitness of test organisms. ANOVA and Student's *t* test as a pairwise post-hoc analysis were used to determine significant differences ($\alpha = 0.05$) between the Al, Fe, and NaCl treatments in average increase in percent survival for organisms added at 8 h after mixing.

Results

Chemistry and toxicity of field-collected samples

Water chemistry parameters for the two upstream stations (LB-4 and PC-5) were as follows: pH, 7.5 and 7.8; conductivity, 298 and 287 μS; alkalinity, 85 and 79 $mg{\cdot}L^{-1}$ as $CaCO_3$; hardness, 125 and 92 $mg{\cdot}L^{-1}$ as $CaCO_3$; Ca^{2+}, 21 and 26 $mg{\cdot}L^{-1}$; and Mg^{2+}, 14 and 8 $mg{\cdot}L^{-1}$.

Water chemistry parameters for the field-collected LB-3 sample were as follows: pH, 2.9; conductivity, 2000 μS; acidity, 625 $mg{\cdot}L^{-1}$ as $CaCO_3$; total Al, 77 200 $\mu g{\cdot}L^{-1}$; total Fe, 24 260 $\mu g{\cdot}L^{-1}$; total Cu, 88.6 $\mu g{\cdot}L^{-1}$; and total Zn, 1251 $\mu g{\cdot}L^{-1}$ (Table 1). Hardness was not determined because of interference in the titration method. Dissolved oxygen concentrations in all field-collected samples were at saturation. All synthesized AMD solutions were made using these water-quality parameters as target values (Table 2). The LB-3 discharge was extremely toxic with a mean ($n = 7$) 48-h LC_{50} value for *C. dubia* of 1.8 ± 1.1% (Table 3).

The three downstream stations had low metal concentrations and near neutral pH values under moderate flow (Table 1). Except for Al at all three stations, metals were below acute water quality criteria (WQC) limits for protection of aquatic life (U.S. EPA 1986). Copper concentrations were below detection limits (1.8 $\mu g{\cdot}L^{-1}$) at the three downstream sites. Alkalinity and hardness values were 42, 32, and 40 $mg{\cdot}L^{-1}$ and 110, 96, and 104 $mg{\cdot}L^{-1}$ as $CaCO_3$ for PC-4, PC-2, and PC-1, respectively. In undiluted samples from these stations, all organisms survived the 48-h tests.

A second set of samples was collected from the field stations under low-flow conditions. Concentrations of Al and Zn were slightly lower in the LB-3 sample compared with the previous sample, the Fe concentration increased slightly, and Cu was below detection limits (Table 1). The pH (3.0) of the sample was slightly higher than that of the previous sample. With lower-flow conditions in the receiving system, Al and Fe concentrations were higher in the three downstream stations than in the previous samples, whereas Zn concentrations were similar. Again, pH values at the stations were near neutral. Alkalinity values were similar to those of the previous samples (48, 40, and 40 $mg{\cdot}L^{-1}$ as $CaCO_3$ for PC-4, PC-2, and PC-1, respectively), but hardness values were not obtained because of interference in the titration method. With increased Al and Fe concentrations, toxicity of the undiluted samples increased, as only 20, 20, and 25% survival were observed in the PC-4, PC-2, and PC-1 samples, respectively, after 48-h.

Synthesized AMD solutions

For the moderately hard synthetic water used as the base in synthesized AMD solutions and as diluent in toxicity tests, the mean pH, conductivity, alkalinity, and hardness were 8.2, 300 μS, 70 $mg{\cdot}L^{-1}$ as $CaCO_3$, and 89 $mg{\cdot}L^{-1}$ as $CaCO_3$, respectively. Concentrations of Ca^{2+} and Mg^{2+} were 18 and 13 $mg{\cdot}L^{-1}$, respectively. These values were similar to those of the receiving system stations LB-4 and PC-5.

In comparing mean LC_{50} values, several synthesized solutions had similar effects to those of the LB-3 sample (Table 3). The S-LB-3 solution, containing all four metals at pH 2.9, and the solutions containing Al–Cu–Zn and Al–Fe at pH 2.9 most closely simulated the actual effluent with LC_{50} values of 2.8, 2.2, and 2.8%, respectively, as compared with 1.8% for LB-3. Although S-LB-3, Al–Cu–Zn, and Al–Fe simulated the actual discharge, the mean LC_{50} for Al alone at pH 2.9 (3.8 %) was not significantly different from that of LB-3. The other six starting solutions had mean LC_{50} values that were significantly higher than that of LB-3, ranging from 4.8% (Fe) to 35.0% (acid alone).

All pH values at LC_{50} concentrations for tests with metals were circumneutral, ranging from 7.4 for Zn to 7.8 for the LB-3 sample (Table 3). The pH values of test concentrations nearest LC_{50} values were taken as estimates of pH at LC_{50} except in the case of the acid-alone solution. The pH at the LC_{50} was not estimated for the acid-alone solution because the LC_{50} was centered between two high-percent dilutions (25% and 50%), and there was a large difference between the mean pH values of the two concentrations.

Based on metals analysis of starting solutions, metal concentrations at LC_{50} values were calculated. For LB-3, S-LB-3, and Al–Cu–Zn solutions, Fe (if present), Cu, and Zn were below WQC limits, whereas Al was above the limits (acute WQC = 750 $\mu g{\cdot}L^{-1}$) at the LC_{50} concentration (Table 4). For tests with individual metals, Al, Zn, and Fe LC_{50}s were above WQC limits, but Fe, at 1160 $\mu g{\cdot}L^{-1}$, was close to the limit of 1000 $\mu g{\cdot}L^{-1}$. Copper has a hardness-based WQC, which at a value of 89 (the mean hardness for diluent water and near the hardness of the field receiving system) is 16 $\mu g{\cdot}L^{-1}$. In tests with copper at pH 2.9 as a starting solution, the LC_{50} was 6.8 $\mu g{\cdot}L^{-1}$, lower than the WQC limit.

Synergism and (or) antagonism in metal mixtures

Calculation of MAI indicated that solutions of Cu–Zn–Fe and Al–Cu–Zn–Fe were less toxic than the sum of their components (antagonistic) with values of –1.502 and –0.560, respectively (Table 5). Confidence limits did not overlap zero so the values are considered significantly different from zero. The remaining four combinations had MAI values ranging from –0.341 (Al–Fe) to 0.290 (Al–Cu–Zn), but confidence intervals overlapped zero for these solutions. Therefore, these metal combinations were considered additive

Table 1. Water-column metals ($\mu g \cdot L^{-1}$), pH, and percent survival of *C. dubia* in full-strength samples from an AMD discharge (LB-3) and from three stations downstream of the AMD-impacted tributary collected under moderate- and low-flow conditions.

Station	Al	Fe	Cu	Zn	pH	% Survival
Moderate flow						
LB-3	77 200	24 260	88.6	1251	2.9	0
PC-4	1 619	482	<1.8	27.7	7.3	100
PC-2	1 110	199	<1.8	26.4	7.5	100
PC-1	913	209	<1.8	31.5	7.7	100
Low flow						
LB-3	60 500	24 390	<0.5	987	3.0	0
PC-4	2 095	1 444	<0.5	16.8	7.2	20
PC-2	2 653	1 504	<0.5	25.8	7.5	20
PC-1	2 512	1 469	<0.5	20.7	7.7	25

Note: AMD, acid mine drainage.

Table 2. Summary of nominal water chemistry parameters for synthetic acid mine drainage starting solutions for whole effluent toxicity tests.

Solution	Al ($\mu g \cdot L^{-1}$)	Cu ($\mu g \cdot L^{-1}$)	Fe ($\mu g \cdot L^{-1}$)	Zn ($\mu g \cdot L^{-1}$)
(1) Al	77 000	0	0	0
(2) Cu	0	89	0	0
(3) Fe	0	0	24 000	0
(4) Zn	0	0	0	1250
(5) Cu–Zn	0	89	0	1250
(6) Al–Fe	77 000	0	24 000	0
(7) Al–Cu–Zn	77 000	89	0	1250
(8) Cu–Zn–Fe	0	89	24 000	1250
(9) S-LB-3	77 000	89	24 000	1250
(10) Acid	0	0	0	0

Note: Conductivity for each solution was approximately 2000 µS, pH was 2.9, and acidity was 500–600 $mg \cdot L^{-1}$ as $CaCO_3$. Metal concentrations are based on those from the LB-3 effluent sample.

Table 3. Mean LC_{50} values (as percent of starting solution) and mean pH values at LC_{50} for field-collected and laboratory-synthesized solutions with various metals.

Starting solution	*n*	Mean ± SD LC_{50} (%)	Significance	pH at LC_{50} ± SD
LB-3 (Al–Cu–Fe–Zn, pH 2.9)	7	1.8 ± 1.1		7.8 ± 0.2
Al, pH 2.9	4	3.8 ± 2.0		7.6 ± 0.2
Cu, pH 2.9	3	7.8 ± 0.8	*	7.6 ± 0.1
Fe, pH 2.9	3	4.8 ± 1.2	*	7.6 ± 0.1
Zn, pH 2.9	3	27.6 ± 6.2	*	7.4 ± 0.1
Cu–Zn, pH 2.9	3	6.4 ± 0.1	*	7.6 ± 0.1
Al–Fe, pH 2.9	3	2.8 ± 1.1		7.6 ± 0.1
Al–Cu–Zn, pH 2.9	4	2.2 ± 0.8		7.7 ± 0.1
Cu–Zn–Fe, pH 2.9	4	7.8 ± 3.1	*	7.7 ± 0.1
S-LB-3 (Al–Cu–Zn–Fe, pH 2.9)	4	2.8 ± 0.5		7.7 ± 0.1
Acid, pH 2.9	3	34.9 ± 0.7	*	N/A

Note: Starting solutions had pH and metal concentrations similar to those in the field-collected sample: pH = 2.90, Al = 77 000 $\mu g \cdot L^{-1}$, Fe = 25 000 $\mu g \cdot L^{-1}$, Cu = 88.6 $\mu g \cdot L^{-1}$, Zn = 1200 $\mu g \cdot L^{-1}$. *n*, number of tests conducted; *, statistically different from LB-3 LC_{50}; S-LB-3, synthesized LB-3, which contained all four metals; SD, standard deviation.

under these testing conditions (i.e., not more toxic than the sum of the individual metals).

Precipitation experiments

In the precipitation experiments, test organisms placed in neutralized Al solutions 8 h after mixing had an average increase in percent survival of 53.0 ± 16.7% compared with those placed into the solution immediately after mixing (Fig. 2). This increase in percent survival was significantly higher ($p < 0.05$) than the difference in survival of organisms added at different times to the NaCl solution (17.3 ± 9.2%), which, as explained previously, should be a measure

Table 4. Mean concentrations and 95% confidence limits (in parentheses) of Al, Fe, Cu, and Zn at LC_{50} values for field-collected (LB-3) and laboratory-synthesized solutions.

Solution	Al ($\mu g \cdot L^{-1}$)	Fe ($\mu g \cdot L^{-1}$)	Cu ($\mu g \cdot L^{-1}$)	Zn ($\mu g \cdot L^{-1}$)
LB-3	1360 (1050–1780)	430 (330–560)	1.5 (1.2–2.0)	22 (17–29)
S-LB-3	1840 (1520–2230)	570 (470–690)	1.9 (1.6–2.3)	54 (45–66)
Al–Cu–Zn	1320 (1110–1590)	—	1.4 (1.1–1.6)	40 (34–48)
Cu–Zn–Fe	—	1570 (1260–1950)	5.3 (4.3–6.6)	135 (108–168)
Al–Fe	2150 (1800–2570)	690 (580–830)	—	—
Cu–Zn	—	—	3.8 (3.5–4.1)	108 (99–117)
Al	2880 (2310–3590)	—	—	—
Fe	—	1160 (950–1480)	—	—
Cu	—	—	6.9 (6.1–7.9)	—
Zn	—	—	—	354 (300–417)
WQC	750	1000	16.0	288

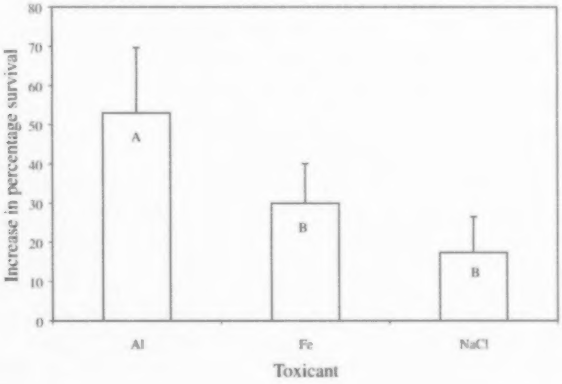
Note: S-LB-3, synthesized LB-3, which contained all four metals; WQC, acute water quality criterion limit.

Table 5. Marking's additive index (MAI) values for synthetic AMD solutions containing two or more metals.

Solution	MAI	(95% CL)	Significance
Cu–Zn	0.169	(–0.063, 0.470)	
Al–Fe	–0.341	(–0.988, 0.119)	
Al–Cu–Zn	0.290	(–0.112, 0.889)	
Cu–Zn–Fe	–1.502	(–2.694, –0.655)	*
Al–Cu–Zn–Fe	–0.560	(–1.289, –0.051)	*
LB-3	–0.123	(–0.783, 0.413)	

Note: A positive MAI value indicates synergism, whereas a negative value indicates antagonism. Ninety-five percent confidence limits (95% CL) that do not overlap zero indicate that MAI value is significantly different from zero. AMD, acid mine drainage; *, statistically different from zero.

Fig. 2. Average (+ standard deviation) difference in percent survival of test organisms placed into solutions immediately after mixing (neutralization) and 8 h after mixing. Different letters indicate significantly different means ($p < 0.05$). Metal concentrations were equal to average 48-h LC_{50} values as calculated in this study, i.e., 2880 $\mu g \cdot L^{-1}$ for Al and 1160 $\mu g \cdot L^{-1}$ for Fe. The sodium concentration was 2.5 $g \cdot L^{-1}$.



of increased organism fitness after 8 h of feeding. The average difference in percent survival between organisms placed into the neutralized Fe immediately and 8 h after mixing was 30.0 ± 10.1%. This value was not significantly different from the value for the salt solution ($p > 0.05$). The average pH values (±SD) for the Al and Fe solutions immediately after mixing were 6.7 ± 0.3 and 6.9 ± 0.4, respectively, and 8 h later, they were 7.4 ± 0.1 and 7.5 ± 0.2, respectively. The average pH for the NaCl solution was 7.9 ± 0.2.

Discussion

AMD is traditionally considered to impact aquatic ecosystems by acidification in combination with dissolved metals, Fe- and Al-hydroxide precipitation covering the stream substrate, and sediment toxicity owing to metals like Cu and cadmium. Our tests with both field samples and laboratory solutions indicate that Al is the primary source of toxicity to *C. dubia* in the circumneutral waters (pH > 7.0) of Puckett's Creek downstream of an acidified tributary with some contribution from Cu, Zn, and Fe. Furthermore, Al is the probable cause of reduced benthic macroinvertebrate diversity with some contribution from Fe and, to a lesser extent, Cu and Zn. In the first set of water samples collected from downstream stations PC-4, PC-2, and PC-1, all test organisms survived, but in the second collection period, samples from all three downstream stations caused acute toxicity to *C. dubia*. Although Cu was below the detection limit and Zn concentrations were lower at all stations in the second set of samples than in the first, the Fe concentration was similar to that in the first sample and Al concentrations were higher in the second set of samples. This result suggests that Cu and Zn are minor toxic factors in this particular system and that Al and Fe are more important. This is in contrast to the finding that Cu and Zn were important in causing toxicity to various fish as components of metal mixtures found in acidified waters (Hutchinson and Sprague 1986; Hickie et al. 1993). Our laboratory tests with 10 different synthesized solutions indicated that mixtures not containing Al had significantly higher mean LC_{50} values than the mean for the field-collected AMD sample (LB-3), whereas none of the solutions containing Al had significantly different LC_{50}s than the LB-3 sample. These data suggest that Al was a more significant contributor of toxicity than Fe in this system.

Although Al is the third most common element in the Earth's crust, its low solubility at circumneutral pH values generally prevents it from being present as a dissolved species at high concentrations in most oxygenated surface waters. However, acidic conditions resulting from acid precipitation or AMD cause dissolution of Al from common minerals. As a result, a number of studies have examined the combined impacts of acid and Al on fish, invertebrates, and plants (e.g., Havas 1985; Burton and Allan 1986; Engleman and McDiffet 1996), but relatively few researchers have documented toxicity resulting from Al at circumneutral pH values. These have consisted of laboratory studies (Havas 1985), studies of alum ($Al_2(SO_4)_3$) treatment (Doke et al. 1995; Smeltzer et al. 1999), and mixing zone studies with fish (Rosseland et al. 1992; Henry et al. 1999). Recent work (Elangoven et al. 1997; Campbell et al. 2000) also indicates that snails bioaccumulate Al, which significantly alters their behavior, by grazing on extracellular mucopolysaccharides that have bound polyhydroxy-Al at neutral pH. Our results provide evidence that Al is contributing to decreased benthic macroinvertebrate diversity and abundance in neutral waters (pH > 7.0) for up to 1 mile downstream of an acidified tributary.

Al has both ionoregulatory and respiratory effects at the gill surface of fish under acidic conditions (Gensemer and Playle 1999). Several authors have suggested that the mode of Al toxicity to fish in mixing zones (pH 5 to 6) is hydrolysis of Al^{3+}; fish gills act as a nucleating surface onto which the hydroxides precipitate, leading to suffocation (Neville and Campbell 1988; Poléo 1995; Exley et al. 1996). In plant roots, however, the tridecameric species $(AlO_4Al_{12}(OH)_{24}(H_2O)_{12})^{7+}$, hereafter referred to as $(Al_{13})^{7+}$, has been experimentally shown to be at least 10 times more toxic than the Al^{3+} species (Parker et al. 1989). Although speculation has been made that $(Al_{13})^{7+}$ may be the toxic form to fish, a direct comparison of $(Al_{13})^{7+}$ and Al^{3+} toxicity to experimental fish suggested that this was not the case (Exley et al. 1994). Aquatic invertebrates are not considered to be as sensitive to Al as fish are, and the toxic effects are generally considered to be of an ionoregulatory nature under slightly acidic conditions (Gensemer and Playle 1999).

Al was measured as total Al in our experiments so it is unknown which species may be the cause of low benthic macroinvertebrate community diversity in Puckett's Creek below its acidic tributary, Lick Branch. Furthermore, we cannot be certain as to whether the toxic mechanism of Al to *C. dubia* was through ionoregulatory or respiratory effects. As waters from Lick Branch (pH ~ 4.5 at the furthest downstream point, Soucek et al. 2000*a*) enter Puckett's Creek, they are quickly neutralized to a pH of greater than 7.0. This rapid increase in pH provides the conditions necessary to form $(Al_{13})^{7+}$ (Parker and Bertsch 1992), which is metastable; substantial concentrations of this species remain in solution 15 min after formation and decrease slowly with time (Parker et al. 1989). Most mixing-zone studies with fish at $pH < 6.0$ indicate that toxicity as the result of hydrolysis of Al^{3+} decreases substantially within 4 to 6 min. In preliminary experiments, we did not observe a reduction in Al toxicity until nearly 8 h after mixing; however, a gross measurement such as mortality may not be sensitive enough to detect slight changes in toxicity resulting from gibbsite ($Al(OH)_3$) formation. Thus, although our time-delayed toxicity test results are consistent with the literature pertaining to Al toxicity in neutral surface waters in that toxicity of the solutions decreased over time, without analytical verification, we can only speculate as to toxic mechanisms and to which Al species is the most toxic to invertebrates at neutral pH.

Our data suggest that Fe can also cause acute toxicity in circumneutral waters downstream of acidified tributaries. Although 7-day LC_{50} values for ferrous iron ranging from 380 to 1620 $\mu g\ Fe(II)\cdot L^{-1}$ have been documented for *C. dubia* in neutralized mine effluents (Milam and Farris 1998), a 48-h LC_{50} value of 1160 μg total $Fe\cdot L^{-1}$ was obtained in the present study. Field-collected samples were only analyzed for total Fe, and although ferrous iron may have been present in the acidic effluent from LB-3, the simulated AMD solutions were made with ferric iron (as $Fe_2(SO_4)_3$). Regardless of the oxidation state of the dissolved Fe species, acute toxicity was observed in neutral waters for both field-collected and laboratory-prepared solutions at total Fe concentrations just above WQC limits. Although the field-collected samples also had high Al concentrations, which were probably responsible for the observed toxicity in the field, our results obtained with simulated Fe solutions suggest that acidified solutions containing only ferric iron may cause toxicity in downstream neutral receiving systems. The time-delayed experiment suggests that ferric iron may have a different mode of toxicity than Al after neutralization as the increase in survival of organisms placed in the solutions 8 h after mixing was not significantly greater than that resulting from increased organism strength alone.

Iron may have another role in the metal mixtures in Puckett's Creek. Our results indicate that two of the synthetic solutions containing Fe (Cu–Zn–Fe and Al–Cu– Z–Fe) were less toxic than the sum of their parts, or the combinations of metals were antagonistic according to their MAI values. The other solution containing Fe in combination with another metal (Al–Fe) had a nominally negative MAI value (suggesting antagonism), but the confidence interval was not significant. These results suggest that in the field situation, Fe in the form of oxyhydroxides may be decreasing the toxicity of metal combinations, perhaps by co-precipitating or adsorbing other metals such as Cu, Zn, and Al (Banks et al. 1997).

Despite the fact that the first sample collected from PC-4 contained Al, Fe, Cu, and Zn at concentrations similar to the toxic concentration as predicted by the LB-3 and S-LB-3 laboratory tests, toxicity was not observed in this sample. These results suggest that WET testing with AMD effluents may not adequately describe in-field impacts; however, the effluents were diluted with U.S. EPA (1993) moderately hard synthetic freshwater containing only deionized water and four salts (KCl, $NaHCO_3$, $MgSO_4$, and $CaSO_4\cdot 2H_2O$). By design, the relative lack of suspended solids and (or) complexing agents in the synthetic water overestimates metal toxicity in laboratory testing to provide a more conservative estimate of in-stream impacts. More complexing agents, such as nitrates, carbonates, fluorides, and dissolved organic carbon, are likely to occur in natural waters such as those of Puckett's Creek, and Al and Cu both are known to form both organic and inorganic complexes, reducing their toxicity (Burton and Allan 1986; McCahon and Pascoe 1989). However, we felt that the moderately hard synthetic freshwater was appropriate for these experiments because most chemical parameters were similar to those for the upstream stations, and our results would be more replicable using this standardized dilution water.

Mechanisms of AMD toxicity are of interest because large sums are being expended to remediate AMD-impacted waters throughout the United States each year by federal agencies (including the Office of Surface Mining and the U.S. Environmental Protection Agency), state agencies in AMD-impacted areas, and local watershed associations. Improved understanding of AMD toxicity mechanisms can allow water quality renovation expenditures to be prioritized and allocated more effectively. Our results suggest that Al and Fe in transition from acidic waters to neutralizing receiving streams cause acute toxicity to standard invertebrate test organisms at pH values greater than 7.0. Aluminum appears to be the cause of benthic macroinvertebrate community impairment in Puckett's Creek for up to a mile downstream of the AMD-influenced tributary, Lick Branch. Although Fe singly may cause acute toxicity in this type of system, it appears to reduce the toxicity of combinations of other metals such as Al, Cu, and Zn. The implication of this research is that agencies hoping to remediate AMD impacts must broaden their scope beyond examination of toxic effects within the zone of pH depression to include downstream reaches of receiving waters.

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Bio-optical characteristics of the snow, ice, and water column of a perennially ice-covered lake in the High Arctic

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Abstract: Lake A is a meromictic, perennially ice-covered lake located at the northern limit of North America (latitude 83°N, Ellesmere Island, Canada). In early June 1999, only 0.45% of incident photosynthetically available radiation (PAR) was transmitted through its 2-m ice and 0.5-m snow cover. Removal of snow from 12 m^2 increased PAR under the ice by a factor of 13 and biologically effective ultraviolet radiation (UVR) by a factor of 16 (from 0.4% to 6.3% of incident). The diffuse attenuation coefficient (K_d) for UVR was substantially lower in the ice than in the underlying freshwater (e.g., 50% lower at 320 nm), indicating the exclusion of chromophoric dissolved organic matter (CDOM) during freeze-up or the subsequent degradation of CDOM retained in the ice. Peak phytoplankton concentrations occurred immediately under the ice, and a broad maximum of photosynthetic sulfur bacteria and associated sulfur particles was observed over the depth interval 20–45 m at <0.005% of incident PAR. Climate-induced changes in the overlying snow and ice have the potential to cause major habitat disruption (UV exposure, PAR, temperature, mixing regime) for these stratified, extreme-shade communities.

Résumé : Le lac A est un lac méromictique couvert de glace en permanence et situé à la limite boréale du continent nord-américain (latitude 83°N, île d'Ellesmere, Canada). Au début de juin 1999, seulement 0,45 % de la radiation incidente disponible pour la photosynthèse (PAR) pénétrait la couche de 2 m de glace recouverte de 0,5 m de neige. Le retrait de la neige sur une surface de 12 m^2 a augmenté la PAR d'un facteur de 13 et la radiation ultraviolette (UVR) à effets biologiques, d'un facteur de 16 (de 0,4 % à 6,3 % de la radiation incidente). Le coefficient d'atténuation (K_d) de l'UVR était considérablement moins élevé dans la glace que dans l'eau douce sous-jacente (e.g. 50 % plus faible à 320 nm), ce qui indique une exclusion de la matière organique dissoute colorée (CDOM) lors du gel ou la dégradation subséquente de la CDOM retenue dans la glace. Les concentrations maximales de phytoplancton se trouvaient juste sous la glace et la densité maximale des bactéries sulfureuses photosynthétiques et des particules de soufre associées s'étalait dans l'intervalle des profondeurs de 20–45 m, à moins de 0,005 % de la PAR incidente. Les changements dans la couverture de neige et de glace générés par le climat peuvent potentiellement causer des modifications majeures de l'habitat (exposition à l'UV, PAR, température, régime de brassage) dans ces communautés stratifiées acclimatées à de faibles intensités lumineuses.

[Traduit par la Rédaction]

Introduction

Perennially ice-covered lakes are an important limnological feature of Antarctica and have proved to be useful model systems for exploring general concepts in geophysics, geochemistry, and microbial ecology. In recognition of this value, a series of such lakes in the McMurdo Dry Valleys region is now the site of a long-term ecological research program (LTER; Priscu 1998). It is less widely known, however, that lakes covered by multiyear ice are also found in the north polar region. Several lakes on northern Ellesmere Island are thought to be perennially ice covered (Ludlam 1996) and other lakes in the High Arctic retain their ice cover throughout summer in some years (e.g., Doran et al. 1996). Our aim in the present study was to evaluate the ice cover and water-column properties of one such north polar lake, Lake A in the Canadian High Arctic, with emphasis on its bio-optical properties relative to analogous lakes in the south polar region.

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Ice and snow cover high latitude lakes for more than 8 months of the year and have a broad range of effects on the physical and biological properties of these ecosystems. The presence of ice isolates the water from wind-induced mixing, and thick snow and ice may also inhibit convective processes. This reduced mixing in turn affects the vertical distribution of gases, nutrients, and planktonic organisms (Wharton et al. 1993; Priscu et al. 1999*a*). The effects of ice and snow cover on radiative transfer also regulate biological productivity by controlling photosynthetically available radiation (PAR), exposure to ultraviolet radiation (UVR), and water temperature. Despite this pervasive influence on limnological processes in northern lakes, little attention has been given to the bio-optics of freshwater ice and snow.

The High Arctic is currently subject to major changes in

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climate. The most striking evidence of change has been in records of the extent and thickness of multiyear sea ice across the Arctic Ocean. Over the period 1978 to 1998, the multiyear sea-ice cover diminished in area by 14% in winter (Johannessen et al. 1999) and by 44% in average thickness during the past three decades (Rothrock et al. 1999). An extensive ice shelf (>10-m-thick sea ice) along the northern coast of Ellesmere Island retreated by 90% over the course of the 20th century, with evidence of substantial thinning of the remaining landfast ice in the 1980s and 1990s (Vincent et al. 2001). Continental High Arctic meteorological records also show evidence of change. Temperature data from Arctic stations over the period 1966–1995 indicate a general warming trend, with the greatest effects in the western Arctic (up to 0.7°C per decade; Weller 1998). There is wide regional variability in precipitation trends, from significant increases at certain locations (e.g., Spitsbergen; Hanssenbauer and Forland 1998) to significant decreases at other sites (e.g., Alaska; Curtis et al. 1998). This climatic change is likely to have an impact on lake ecosystems via shifts in snow and ice cover (e.g., Doran et al. 1996) and highlights the need for improved understanding of the properties of these lake ecosystem components.

The High Arctic is also experiencing changes in its incident UV radiation flux. During spring, the increases in surface erythemal UVR resulting from severe chemical ozone losses observed in the Arctic during winter are estimated to be about 22% relative to the values in the 1970s (Madronich et al. 1998). This increase is likely to worsen in duration and severity in the future, in part associated with greenhouse gas effects on stratospheric cooling (Shindell et al. 1998).

Although many modeling and field studies have addressed the variations of snow and ice albedo, little is known about the transmission of UVR through snow and freshwater ice, and even the PAR attenuation characteristics of these media are poorly understood. Clean, fresh, cold snow has a high albedo (>0.9) and is therefore relatively opaque to PAR (Perovich et al. 1998); however, during the aging of the snow or when it becomes wet or covered by wind-blown particles, the PAR albedo can drop substantially (Grenfell and Maykut 1977; Perovich et al. 1998). The UVR albedo of snow is lower than that for PAR (Perovich et al. 1998). The measured diffuse attenuation coefficients for PAR, K_d(PAR), of snow are highly variable depending on snow density, grain size, temperature, and wetness (Thomas 1963; Grenfell and Maykut 1977). To our knowledge, no K_d(UVR) values for snow have been published to date. K_d(PAR) of thick perennial ice has been reported to be as low as 0.2 m^{-1} for Antarctic lakes (Howard-Williams et al. 1998), and transmission of incident PAR through snow-free, 1.5- to 2.2-m-thick clear ice was shown to be as high as 21–35% for High Arctic lakes (Welch and Kalff 1974; Bolsenga et al. 1996). The limited available literature (Ellis-Evans et al. 1998; fig. 4 in Howard-Williams et al. 1998) suggests that UVR transmission through clear ice can be of the same order of magnitude, or greater, than PAR transmission. This may result from the strong within-ice attenuation of the red part of the PAR spectrum. Kepner et al. (2000), however, found low UV transmission through the ice cover of Lake Hoare in the McMurdo Dry Valleys (<0.6% at 320 nm), and this was attributed to the extremely degraded, highly scattering ice surface and the high concentrations of sediment on and within this 4- to 5-m-thick ice. Significant under-ice UVR has been measured in other Antarctic Dry Valleys lakes despite >3-m-thick ice (Vincent et al. 1998); however, there have been no equivalent measurements in Arctic freshwater ecosystems.

In the present study, we addressed the hypothesis that High Arctic lakes may be sensitive to environmental change by virtue of their overlying snow and ice. We undertook measurements of UVR and PAR transmission through the snow and ice cover and of optical properties of the underlying water column of perennially ice-covered Lake A on northern Ellesmere Island. We selected Lake A because it lies at the northern limit of Arctic lakes where future climate changes and ozone depletion are likely to be pronounced.

Materials and methods

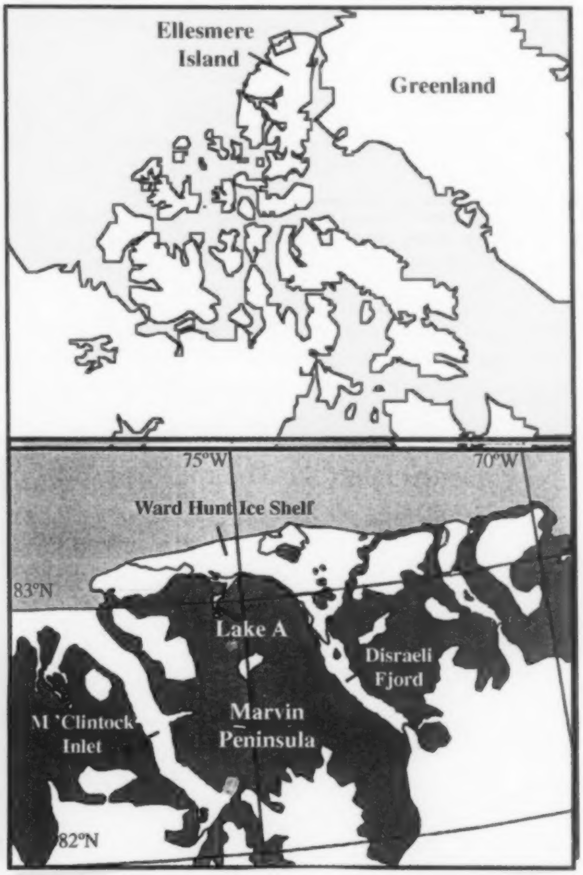
Study site

Lake A is located on northern Ellesmere Island (83°00′N, 75°27′W; Fig. 1) in a polar desert region with mean annual precipitation of 157 mm and mean annual temperature of −17.9°C (Table 1). This precipitation is much greater than that in the McMurdo LTER (≤50 mm) at a comparable latitude in Antarctica (78°S), but the mean annual temperature is similar to that in the McMurdo lakes region (−17°C to −19°C; Doran et al. 1994). Table 1 summarizes the mean values for climate variables for the period 1951–1999 at Alert, the nearest available meteorological station, 180 km from Lake A (no local data are available as yet from the lake basin). Lake A was first sampled in 1969 by Geoffrey Hattersley-Smith's group (Hattersley-Smith et al. 1970) and was the object of work in 1982 (Jeffries et al. 1984) and 1993 (Ludlam 1996). The lake depth is >115 m (deepest measured point) and has an area of 4.9 km^2 and a glacier-free drainage basin with an area of 36 km^2. A short outlet stream flows from the northernmost point of the lake to an epishelf lake dammed by the Ward Hunt Ice Shelf. The lake is 3.3 m above sea level and was cut off from the sea following isostatic uplift approximately 3000 years ago, thereby producing the current meromictic conditions (Hattersley-Smith et al. 1970; Jeffries et al. 1984). The conductivity of the monimolimnion is approximately the same as seawater and its ionic composition is that of modern ocean water although modified by biological activity; it is depleted in sulfate and enriched in dissolved inorganic carbon by microbial activity (Jeffries et al. 1984). The monimolimnion and mixolimnion are separated by a chemocline that extends from 7 to 25 m. A thermal maximum of 8–9°C occurs at ~15 m and the waters are anoxic below 14 m (Ludlam 1996). Lake A is covered by 2-m-thick ice, with a candled ice surface resulting from the summertime partial melting (Hattersley-Smith et al. 1970). A narrow moat opens around the ice pan during summer, at least in some years. On August 5, 2001, the moat was 1–10 m wide, except on the eastern side of the lake at the site of the main inflowing stream where the moat was about 100 m wide (C. Belzile and P. Van Hove, personal observation). RADARSAT data for one of the warmest summers on record (1998; Vincent et al. 2001) show the persistence of Lake A ice in late August, whereas the nearby Taconite Inlet lakes (40 km southwest of Lake A) lost their ice cover (Fig. 2). However, the moat on the northern shore of Lake A was much wider (30–120 m; Fig. 2) than observed in 2001. Lake A was covered by ice during late summer, or candled ice was present under the snow in early summer (indicating multiyear ice cover), on each of 11 years of observations during the period 1950–2001.

Sampling

Lake A was sampled during the period of 3–8 June 1999. This time of the year is characterized by continuous daylight and the solar

Fig. 1. Map showing the location of Lake A, northern Ellesmere Island, Canada.



elevation varies from 13 to 33° over the 24-h cycle. Air temperatures at Alert varied from –0.5°C to –10.5°C during the 6 days. Water samples were obtained from 25 selected depths over the deepest part of the lake using a Kemmerer sampling bottle (length = 31 cm) and were stored in dark Nalgene bottles until filtration 1–3 h later at our base camp. Profiles of temperature, specific conductivity, and dissolved oxygen were made using a Hydrolab Surveyor 3 (Hydrolab Corp., Austin, Tex.). Data were recorded at discrete depths to allow stabilization of the instrument; measurements were made every metre from 2 to 13 m and every 50 cm down to 47.5 m (the full length of the profiler cable). Specific conductivity readings were converted to salinity using the algorithm of Fofonoff and Millard (1983). This algorithm is the equation of state for seawater and is applicable over the salinity range of 2–40. Terrestrial input, differential diffusion, and biological processes will alter the ionic composition of the water, but with the exception of the surface waters, this variation should be minor considering that the water in the lake is largely marine derived (Jeffries et al. 1984). The thickness of the ice was measured in five holes distributed over the central region of the lake (spaced by at most 500 m). Snow depth was measured at the site of transmittance measurements ($n = 15$ over a 12-m^2 area) and every 1 m along a 20-m transect nearby this site. All optical measurements (described below) were made within 5 h of local noon (solar elevation between 25 and 33°) during clear sky conditions or high light clouds.

Albedo measurements

The snow and cleared-ice albedo ($\alpha(\lambda)$), i.e., the ratios of upwelling irradiance (E_u) to downwelling irradiance (E_d), were measured using a PUV510 radiometer (Biospherical Instruments, Inc., San Diego, Calif.) at the same site as the transmittance measurements (see below). The PUV510 measured cosine-corrected UVR at 305, 320, 340, and 380 nm (full bandwidth at half maximum of 8–10 nm) and PAR (400–700 nm). The radiometer was mounted on a 3-m-long pole, which allowed the measurement of E_d and E_u at a height of 1 m over the snow or ice surface.

Irradiance transmittance through the ice and snow cover

The transmittance of the snow and ice ($T(\lambda)$) was calculated as the ratio of downwelling irradiance of wavelength λ at the lower surface of the ice ($E_d(z_{ice}, \lambda)$) to the incident irradiance ($E_d(0^+, \lambda)$). Transmittance depends on the specular and volume components of the albedo and on the attenuation of irradiance by snow and ice according to Beer's Law. For these transmittance measurements, the PUV510 was installed in an unshaded location on the lake ice, and an underwater radiometer (PUV500, Biospherical Instruments, Inc.) was positioned to measure simultaneously the cosine-corrected, under-ice irradiance. The PUV500 recorded irradiance at the same wavelengths as the PUV510 and also recorded depth and temperature. Underwater irradiance measurements were corrected for dark current by subtracting the value obtained at in situ temperatures within the water column after fitting the radiometer with a light-tight Neoprene cap. The PUV500 radiometer was positioned under the ice through a 65-cm-diameter hole using an articulated arm designed in our laboratory. The aluminum arm allowed the positioning of the radiometer flush with the lower ice surface at a distance of 1 m from the hole. During the measurements, the hole was tightly covered with an opaque plastic board, 1 m^2 in area, to prevent direct solar radiation from entering the ice sheet through the hole. Great care was taken to preserve the integrity of the snow cover over the area where the measurements were made in order to obtain transmittance through the natural ice and snow cover. The snow cover was then removed from an area of 12 m^2, and the measurements were repeated under that area to estimate transmittance of only the ice.

Snow and ice attenuation coefficients

The attenuation of irradiance in ice calculated from radiative transfer models is often characterized by the asymptotic extinction coefficient $K_{asym}(\lambda)$ (e.g., Grenfell 1991). In an optically thick medium, the asymptotic state, where the shape of the light field is axially symmetric and does not change, should be approached far from the upper boundary. $K_{asym}(\lambda)$ is difficult to measure in the field and small-scale variability in the physical, biological, and thus optical properties of the ice makes it difficult for the light distribution to remain in the asymptotic state (see Perovich et al. 1998). One simpler way of characterizing irradiance attenuation in ice from field measurements is the "effective" extinction coefficient (Grenfell 1991). This effective downwelling diffuse attenuation coefficient ($K_d(\lambda)$, m^{-1}) for ice can be calculated as

$$(1) \qquad K_d(\lambda)_{ice} = -\ln(E_d(\lambda, z_{ice})/E_d(\lambda, 0^-))/z_{ice}$$

where $E_d(\lambda, z_{ice})$ is the under-ice downwelling irradiance measured in the absence of snow and $E_d(\lambda, 0^-)$ is the downwelling irradiance just below the surface given by

$$(2) \qquad E_d(\lambda, 0^-) = E_d(\lambda, 0^+)\ (1 - \alpha(\lambda)_{ice})$$

where $\alpha(\lambda)_{ice}$ is the albedo of the ice surface (Grenfell 1991). Knowing $K_d(\lambda)_{ice}$, snow $K_d(\lambda)$ can similarly be calculated as

$$(3) \qquad K_d(\lambda)_{snow} = -\ln(E_d(\lambda, z_{snow})/E_d(\lambda, 0^-))/z_{snow}$$

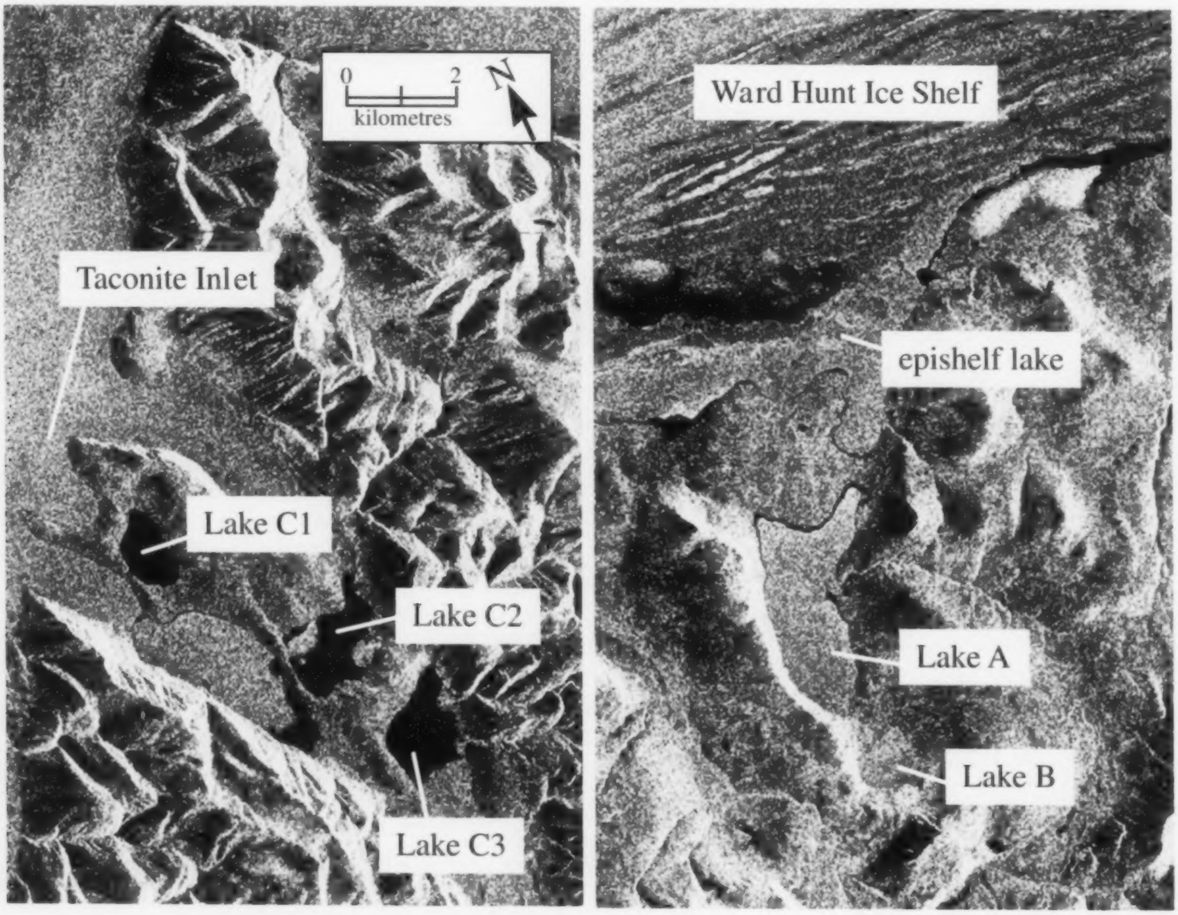
where $E_d(\lambda, z_{snow})$ is the spectral downwelling irradiance at the snow–ice interface given by

Table 1. Mean, minimum, and maximum for meteorological data from Alert over the period 1951–1999.

	Mean	Minimum	Maximum
Precipitation (mm)	157	93	291
Temperature (°C)	–17.9	–19.5	–15.8
Onset of melt (date)	17 June	4 June	1 July
Onset of freeze (date)	21 August	7 August	5 September
Length of melt season (days)	65	43	85
Freezing degree-days	6736	5988	7247
Thawing degree-days	200	104	336

Note: Following Rigor et al. (2000), the length of the melt season was computed from the daily average temperature by using a 2-week running mean filter and defining the onset of melt and freeze as the day that the filtered data rose or dropped below the melting temperature of snow and freshwater ice (0°C).

Fig. 2. RADARSAT-1 images of northern Ellesmere Island acquired on 30 August 1998. On the right, ice-covered Lake A and Lake B are shown. For comparison, on the left, ice-free lakes of the Taconite Inlet region, 40 km to the southwest of Lake A, are shown.



$$E_d(\lambda, z_{snow}) = E_d(\lambda, z_{ice})/(\exp(-K_d(\lambda)_{ice} z_{ice}) \quad (4)$$

and $E_d(\lambda, 0^-)$ is equal to $E_d(\lambda, 0^+)$ multiplied by $1 - \alpha(\lambda)_{snow}$.

Water-column irradiance profiles

UVR and PAR under-ice profiles were measured over the deepest part of the lake, with natural snow-cover conditions, using the same PUV500 radiometer as used for transmittance measurements. The PUV500 gave ~15 data points per metre during profiling. Underwater irradiance measurements were corrected for dark current by subtracting the minimum asymptotic value reached at depth. The PUV500 radiometer was lowered through the hole used for $T(\lambda)$ measurements, which was tightly covered with a 1 m^2 opaque board to prevent direct solar radiation from entering the water column through the hole. $K_d(\lambda)$ for the surface freshwater (2–5 m, the 0-m depth being the piezometric water level in the hole) was determined by linear regression of the natural logarithm of $E_d(\lambda, z)$ versus depth. A vertical profile of the scalar PAR attenuation coefficient (K_0(PAR), m^{-1}) was calculated from E_0(PAR) measured using a PNF300 radiometer (Biospherical Instruments, Inc.). K_0(PAR) was calculated for every 0.5-m interval from the surface to 23 m (the detection limit of the instrument). The beam attenuation coefficient at 660 nm, beam c(660) (m^{-1}), was measured using a Sea Tech transmissometer (Wet Labs, Inc., Philomath, Oreg.) measuring transmission of a collimated light beam over a 10-cm path length.

Chlorophyll *a*

Water samples collected at every metre in the oxic zone (2–12 m) were vacuum-filtered through a 25-mm GF/F-equivalent filter (MFS GF75; Advantec MFS, Inc., Dublin, Calif.). Additional samples were prefiltered through 2-μm Nuclepore filters (Nucleopore Corp., Pleasanton, Calif.) and then onto MFS filters to obtain the picoplanktonic fraction. Filters were stored at –20°C until measurement of chlorophyll *a* (Chl *a*). Chl *a* was extracted with boiling 95% ethanol (Nusch 1980), and the fluorescence of the extract was measured with a model 450 Sequoia–Turner fluorometer (Sequoia–Turner Corp, Mountain View, Calif.). Phaeopigments were corrected for by acidification. For samples collected in the anoxic zone, the absorbance of ethanol extracts of pigments collected on GF/F-equivalent filters was measured using a Hewlett-Packard 8452A diode array spectrophotometer (Hewlett-Packard Corp., Palo Alto, Calif.).

Particulate absorption coefficient

Water samples from selected depths (2, 6.5, 12, 22, and 29 m) were vacuum-filtered in duplicate through 25-mm GF/F filters and stored at –20°C until measurement (10 days after collection) of spectral absorption by particles (a_p). The absorbance of particles concentrated onto the filters was measured every 2 nm over the spectral range 390–800 nm according to Roesler (1998) using a Hewlett-Packard 8452A diode array spectrophotometer equipped with an integrating sphere (Labsphere RSA-HP-84; Hewlett-Packard Corp.). Absorbance values were then converted to a_p using the algorithm of Roesler (1998).

Chromophoric dissolved organic matter (CDOM) absorption coefficient

Measurements of the CDOM absorption coefficient, a_{CDOM} (m^{-1}), were made on each water sample and also for a melted-ice sample taken at ~0.7 m below ice surface and slowly thawed in the dark at 4°C in a plastic Ziploc® bag (S.C. Johnson & Son, Inc., Racine, Wis.). Initial meltwater from this ice sample was discarded to remove any contaminant that may have been transferred during ice drilling and handling. Samples were filtered through 0.22-μm Sartorius cellulose acetate filters (Sartorius, Goettingen, Germany) and stored at 4°C in acid-cleaned, amber glass bottles until analysis (within 4 months). a_{CDOM} was measured every 2 nm over the wavelength range 250–820 nm using a 1-cm, acid-cleaned, quartz cuvette in a Hewlett-Packard 8452A spectrophotometer.

Dissolved organic carbon analysis and CDOM characterization

Dissolved organic carbon (DOC) concentration was determined using the UV Digestion and Infra-red Detection method (Environment Canada, National Laboratory for Environmental Testing). CDOM characterization was made using synchronous fluorescence spectroscopy (Senesi et al. (1991) as modified by J.A.E. Gibson et al., unpublished data). Synchronous fluorescence spectra were recorded with a Shimadzu FR5000 spectrofluorometer (Shimadzu, Kyoto, Japan) used in the synchronous mode with a slit width of 5 nm on both sides and a wavelength difference between the excitation and emission beams of 14 nm, which we have found to be optimal for resolving differences in CDOM between sources. This setting also minimizes the overlap between CDOM peaks and the Raman water peak. Spectra were recorded over the excitation wavelength range 200–600 nm with a corresponding emission range of 214–614 nm. Previous analysis of water samples or isolated fulvic acids from >50 aquatic environments showed that small, autochthonous-like molecules of CDOM (simple aromatic rings without further conjugation) usually show a strong fluorescence peak at 293–308 nm and often show secondary peaks around 360 nm, whereas higher molecular weight molecules with more complex fluorophores (allochthonous-like humic and fulvic materials) fluoresce at longer wavelengths (J.A.E. Gibson et al., unpublished data).

Results

Ice- and snow-cover properties

At the time of sampling, Lake A was covered by 1.97 m (standard deviation (SD) = 0.01 m) of ice. The top 0.12 m was candled ice with long crystals several centimetres in diameter, and the rest was completely fused and clear. No white ice or troughs or ridges at the ice surface were observed. The maximum height of relief on the smooth ice surface was of the order of 10 cm. The top metre of clear ice contained large flattened air bubbles (up to 6 cm long, a few centimetres wide, but only a few millimetres thick). Bubbles were rare and smaller deeper in the ice sheet. Sediment was distributed throughout the top metre of the ice, forming aggregates up to 2 cm in diameter. The piezometric water level was ~13 cm below the ice surface. The snow depths at 1-m intervals along a 20-m transect varied from 39 to 58 cm (average 52 cm, coefficient of variation (CV) = 9%), and the snow surface was flat. At the site of transmittance measurements, the ice was overlaid by 41 cm (CV = 8%, n = 15) of snow. The top ~30 cm was composed of fresh snowflakes and small-grained snow. The deeper layers were composed of loose large crystals typical of deep hoar and indicative of temperature-gradient metamorphism. The average snow density over the full snow profile was 0.21 $g \cdot cm^{-3}$ (as measured gravimetrically using a 6.4-cm-diameter cylinder). The weight of that snow would depress the ice surface by 10 cm. Given the piezometric water level of 13 cm, an average ice density of 0.88 $g \cdot cm^{-3}$ can be deduced.

Irradiance transmittance through the ice and snow cover

The transmittance of PAR and discrete UV wavelengths through the intact ice and snow cover and %*T* through the ice for a 12-m^2 area cleared of snow are shown in Fig. 3*a*. In presence of the snow cover, 0.45% of incident PAR was transmitted. In the UVR waveband, %*T* decreased slightly with decreasing wavelength, from 0.46% at 380 nm to 0.31% at 320 nm. Under-ice E_d(305) was below the PUV500 detection limit, preventing %*T*(305) determination. Removing the snow greatly increased the transmittance; 5.7–6.6% of incident irradiance was transmitted through the ice. The increase was greater at shorter UV wavelengths; this removal of the snow cover resulted in an 18-fold increase in UV at 320 nm and 13-fold in PAR transmittance. Under the conditions of almost eliminated snow cover, the transmittance of 340 nm and 380 nm UV-A was higher than that for

PAR. To calculate the integrated photoinhibiting irradiance prevailing just under the ice, we extended the UVR transmission from the three wavelengths measured by the PUV500 over the full UV spectrum and applied this modeled transmission to the spectral incident irradiance prevailing at noon. This under-ice irradiance was weighted with the biological weighting function for inhibition of photosynthesis from Cullen et al. (1992). Under natural conditions, the weighted under-ice irradiance was only 0.4% of incident. The almost complete removal of snow cover increased photoinhibiting irradiance to 6.3% of incident, a 16-fold increase.

An important part of the difference in %*T* between natural snow conditions and cleared ice was caused by changes in the albedo of the surface. The snow albedo was very high and showed little spectral dependence, varying from 0.94 at 320 nm to 0.97 for PAR (Fig. 3*b*). Once the snow had been removed, the albedo of the candled ice varied from 0.73 at 320 nm to 0.84 for PAR (Fig. 3*b*). Removing the snow cover thus decreased the albedo by 20–22% in the UVR and 13% in the PAR range.

Water-column properties

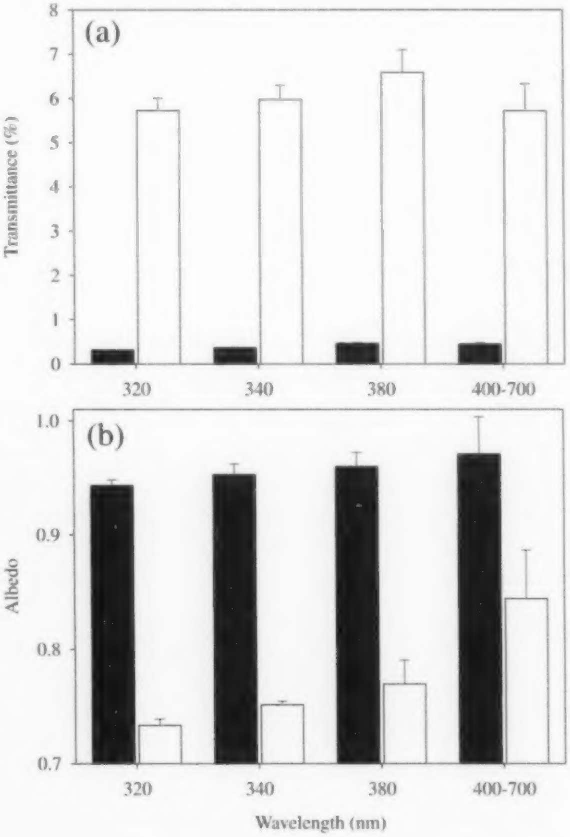
The vertical profiles of temperature, salinity, and dissolved oxygen showed that the water column was highly stratified (Fig. 4). The top 10-m section of the profile was freshwater with moderately low conductivity (minimum of 0.27 $mS \cdot cm^{-1}$). A chemocline with increasing salinity extended from 10 m to ~28 m; below this depth, the salinity reached ~90% of seawater. The oxic zone extended to 13 m; the percent of oxygen saturation was 120–133% in the top 9 m (probably influenced by oxygen exclusion during ice formation, Wharton et al. 1993) and dropped to 9% at 13 m. Although water temperature was near freezing just under the ice, a thermal maximum of 8.75°C was located at 17.8 m. In the monimolimnion, water temperature gradually decreased with depth to a measured minimum of 4.0°C. The profiles showed no evidence of a mixed isothermal or isohaline layer at any depth.

Spectral irradiance attenuation in the water column

Despite low absolute values, complex patterns of variation of beam*c*(660) were observed down through the water column (Fig. 5). An upper maximum was observed just under the ice, and a second peak began at 29 m and extended to 45 m. A series of irregular, localized peaks were also measured between 12 and 20 m; these peaks are likely associated with Schlieren effects caused by changes in refractive index resulting from the mixing of waters of different salinity during the lowering of the profiler. Below 60 m, beam*c*(660) showed little variability and was slightly higher than the value encountered at 15–20 m. The insert in Fig. 5 compares our beam*c*(660) profile to the one of Ludlam (1996). The large peak measured between 10 and 20 m in late May 1993 was absent in 1999. Also, in 1993, the near-surface maximum was observed very close to the lower ice surface and was only ~1 m thick.

The water column values of $K_d(\lambda)$ were in the low to moderate range for lake waters. The K_d values for UVR in the surface 5 m of the water column were 1.65 (0.28), 1.33 (0.06), and 0.80 (0.10) m^{-1} at 320, 340, and 380 nm, respectively (means of five profiles, SD in parentheses). The equivalent value for PAR was 0.352 (0.089) m^{-1}. In the absence of ice, the 1% depth of 320 nm and 380 nm UVR would be 2.8 m and 5.7 m, respectively, whereas the 1% depth of PAR would be 13.1 m. The large vertical variability in K_0(PAR) matched the beam*c*(660) profile (which is independent of the natural irradiance field), with maximum attenuation just under the ice ($K_0(\text{PAR}) = 0.347$ m^{-1} over the 2- to 5-m depth interval) and lower attenuation between 7 and 14 m (Fig. 6). Only 0.03% of incident E_0(PAR) reached the top of the photosynthetic sulfur bacteria distribution at 16 m (see below) and less than 0.003% at 29 m, the depth of the beam*c*(660) maximum (Fig. 6).

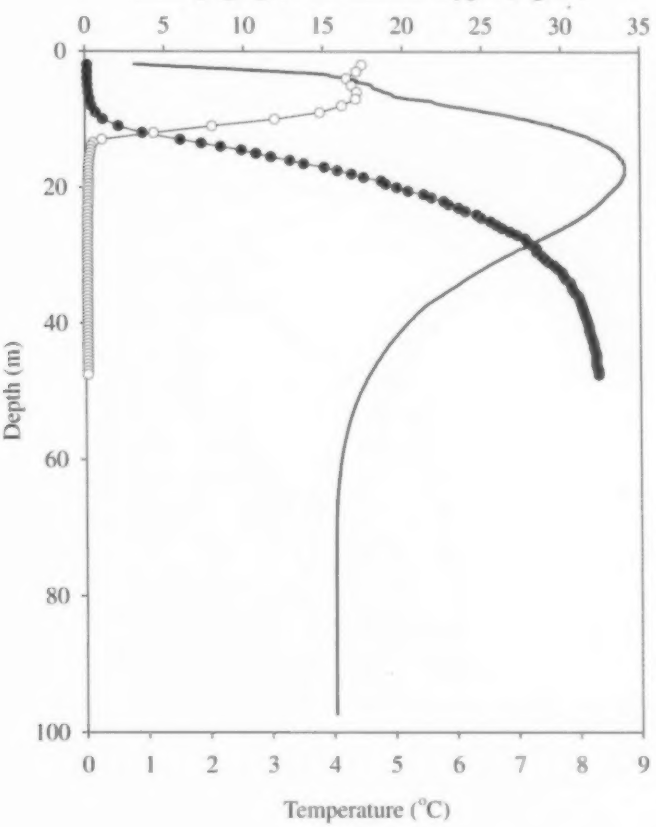
Fig. 3. (*a*) Transmittance through the snow and ice cover (solid bars) of Lake A and through the ice cleared of snow over a 12-m^2 area (open bars). Error bars denote standard deviation (SD) on means from 3 and 4 measurements, respectively. (*b*) Albedo of the snow (solid bars) and candled ice (open bars) surfaces of Lake A. Error bars are SD for 2 and 3 replicated measurements, respectively.



Vertical distribution of optically active particulate and dissolved organic matter

Variations in a_p (Fig. 7) were consistent with the vertical pattern in beam*c*(660). At 22 m, the a_p spectra showed a large absorption peak at 715 nm, typical of bacterio-

Fig. 4. Temperature (thick line), salinity (solid circles), and dissolved oxygen (open circles) profiles in the water column of Lake A. Salinity and dissolved oxygen were measured using an Hydrolab profiler and temperature was measured using a PUV500.

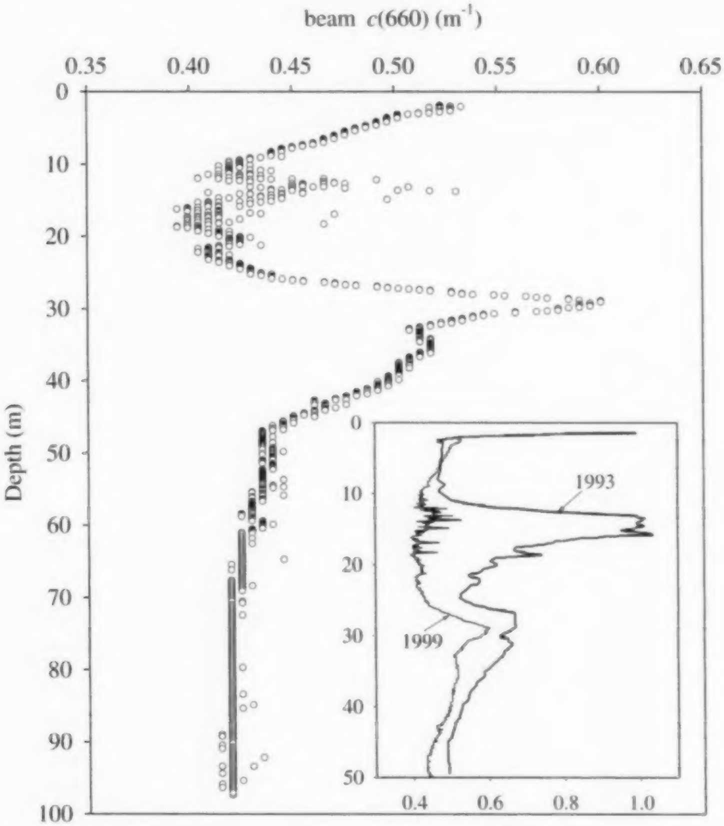


chlorophyll *e* (BChl *e*). The BChl *e* identification was confirmed using methanol extracts and showed the red absorption peak to be centered at 659 nm (Stal et al. 1984). The absorbance of ethanol extracts indicated the absence of BChl *e* above 16 m and maximum concentrations between 20 m and 30 m. The source of this BChl *e* is likely to be green photosynthetic sulfur bacteria of the genus *Chlorobium* (Holt et al. 1993). The absorption maximum found at 29 m (more than two orders of magnitude higher than the a_p measured at other depths; Fig. 7) is probably due to particles of elemental sulfur that accumulate outside these bacterial cells (Holt et al. 1993) superimposed on the BChl *e* absorption peak and possibly also the formation of iron oxides during filtration. The highest a_p in the upper freshwater section of the water column was found just below the ice at a depth of 2 m. The spectral shape of a_p in this oxic zone was typical of phytoplankton, with the red absorption peak at or close to 672 nm, indicative of Chl *a*. The primary Chl *a* absorption maximum was in the blue region of the spectrum, as expected, with an additional broad peak of absorption in the range 530–580 nm, indicative of carotenoids and possibly phycoerythrin (epifluorescence microscopy showed the presence of picocyanobacteria; P. Van Hove et al., unpublished data). The detailed Chl *a* profile in the oxic waters confirmed that Chl *a* concentration was maximal just under the ice (0.43 μg·L^{-1}) and declined steadily with depth to reach 0.07 μg·L^{-1} at 12 m. On average, 62% of the total Chl *a* was contributed by the <2 μm fraction (range 39–97%).

DOC concentrations were low in the upper freshwaters, varying from 0.6 to 1.3 mg·L^{-1} with maximum concentrations just under the ice (Fig. 8). In the monimolimnion, DOC concentrations increased rapidly to reach 3–4 mg·L^{-1}; these DOC concentrations are high considering the extreme high latitude position of the lake (cf. Vincent et al. 1998). The vertical distribution of $a_{\mathrm{CDOM}}(320)$ followed that of DOC (Fig. 8). However, the DOC-specific $a_{\mathrm{CDOM}}(320)$ was low in the freshwater layer (2–3 m^{-1}(mg·L^{-1})$^{-1}$) and increased to 4–5 m^{-1}(mg·L^{-1})$^{-1}$ in the monimolimnion. The much more colored DOC in the monimolimnion suggests a different composition of the DOC pool given that high DOC-specific absorption is usually associated with allochthonous DOC (Morris et al. 1995).

The synchronous fluorescence scans provided further insights into the chemical composition of the DOC and CDOM (Fig. 9). A fluorescence peak occurred at 293–308 nm, indi-

Fig. 5. Beam *c*(660) profile measured on June 7th, 1999. The insert shows the comparison with Ludlam's (1996) profile measured on May 26, 1993.



cating that the CDOM in the mixolimnion (Fig. 9*a*) was essentially from microbial origin, in agreement with the low DOC-specific a_{CDOM}. The CDOM in the ice (0.7 m below ice surface) showed a large peak centered at 293 nm that was not found in the scans of samples from the underlying water column. $a_{CDOM}(320)$ in the ice was 1.75 m^{-1}; this value is about half that measured just under the ice and slightly lower than the minimum value measured in the water column (1.85 m^{-1} at 10 m, Fig. 8). From 12 to 20 m, where the brackish waters were suboxic or anoxic, the fluorescence spectra showed a large peak with a maximum at 362 nm and high fluorescence per unit DOC (Fig. 9*b*). Samples from 25 m to the bottom had two additional peaks centered at 392 nm and 491 nm, indicative of large, complex molecules (Fig. 9*c*).

Comparison of snow, ice, and water K_d

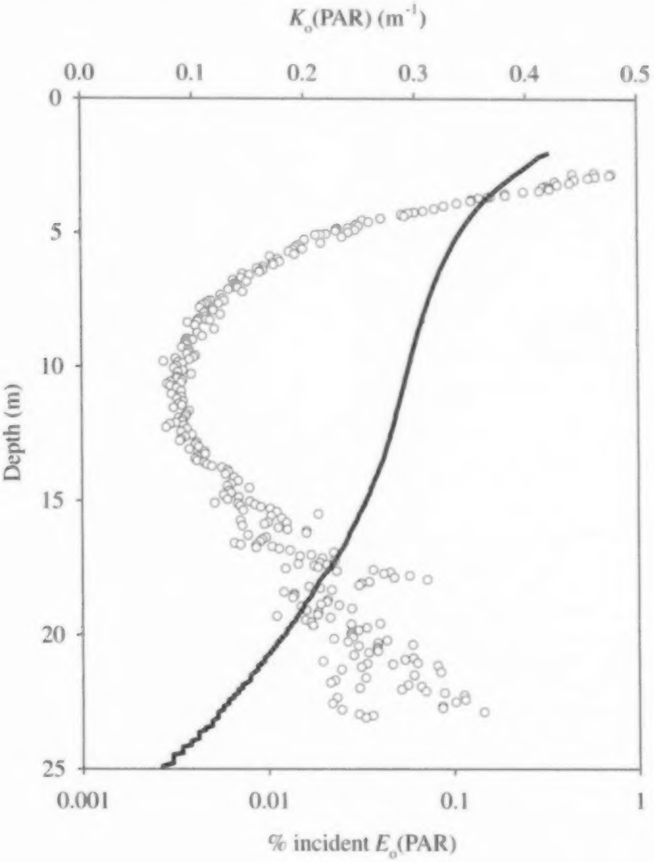
Snow K_d(PAR) was 2.1 m^{-1} (Fig. 10*a*), almost an order of magnitude lower than values previously reported (Thomas 1963; Grenfell and Maykut 1977). This striking difference probably results from the low attenuation in the deep hoar layer of the Lake A snow. Snow K_d(UVR) increased with decreasing wavelength to reach 3.3 m^{-1} at 320 nm. Attenuation in the ice was very low compared with that in the snow. Ice K_d(PAR) was 0.32 m^{-1} and K_d increased slightly with decreasing wavelength in the UVR (Fig. 10*a*). The K_d(UVR) for the ice was strikingly lower (up to 53%) than that of the water column, whereas the K_d(PAR) in the ice was 45% higher than in the water column (Fig. 10*b*). Our method of calculation resulted in low effective K_d values for snow and ice. To calculate $K_d(\lambda)_{ice}$, some authors (e.g., Fritsen et al. 1992), rather than using eq. 2, assumed that $E_d(0^-)$ is determined by the specular reflection of $E_d(0^+)$, i.e., $E_d(0^-)$ is approximated to be equal to the incident irradiance reduced by only 2–5%. $K_d(\lambda)_{ice}$ calculated with this $E_d(0^-)$ gives values about two times higher than those calculated using our equations, although the resulting ice $K_d(320)$ is still lower than that of the water column. In the water column, CDOM was responsible for most of the UV and blue light absorption; for example, at 440 nm, CDOM absorption was 0.45 m^{-1} just under the ice, whereas absorption by particles was only 0.04 m^{-1}.

Discussion

Life at the northern limit of lakes

In a previous limnological study of Lake A, Ludlam (1996) suggested that a supersaturated oxygen maximum found just under the ice was related to phytoplankton photosynthesis

Fig. 6. Attenuation coefficient for scalar photosynthetically available radiation (K_0(PAR); open circles) and percent of incident scalar PAR down the water column (thick line). K_0 was determined for 0.5-m depth intervals.

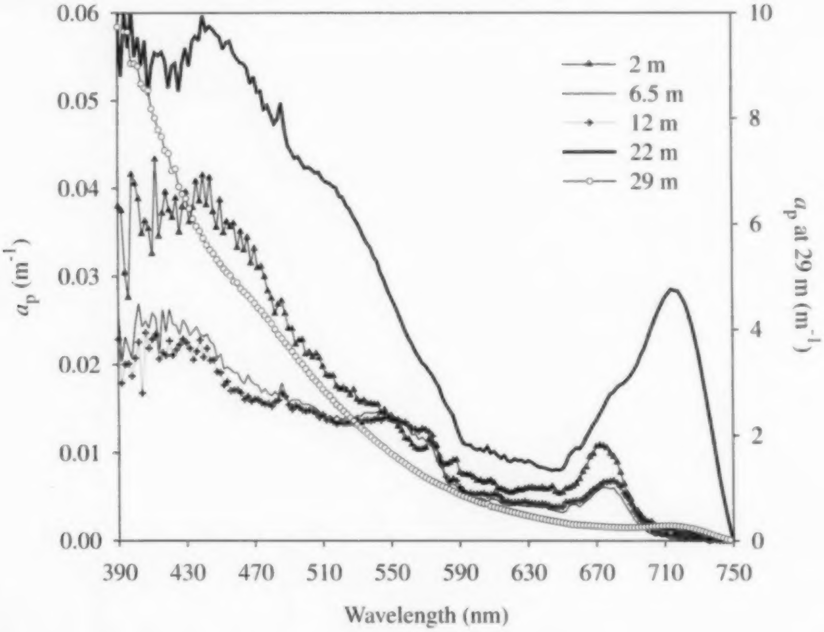


and the deep turbidity maximum was likely due to anoxygenic phototrophic bacteria. The a_p spectra presented here confirm the presence of these hypothesized microbial assemblages and indicate that the deep maximum is dominated by *Chlorobium*. Despite its extreme northern location and thick perennial ice cover, Lake A is inhabited by a complex community of prokaryotic and eukaryotic autotrophs. These autotrophs support an assemblage of small-sized copepods with a mean density of ~400 individuals·m^{-3} in the top 23 m (Van Hove et al. 2001). The presence of macrozooplankton in Lake A represents one important difference relative to the McMurdo LTER perennially ice-covered lakes (Priscu et al. 1999*a*). The low Chl *a* biomass that we measured may be partly due to grazing by copepods, although it may also be related to our sampling early in the growing season. The migration of zooplankton through the water column and their production of fecal pellets is a transport mechanism for organic material in this lake that is absent from the McMurdo lake ecosystems. The bio-optical properties of Lake A's snow and ice cover exert a major influence on all of these planktonic communities by controlling the biological UV exposure and the availability of solar energy for photosynthesis. The large bio-optical and other limnological variations down the water column of Lake A parallel the conditions found in the McMurdo lakes. In these Antarctic systems, as in Lake A, there are major changes in temperature, salinity, and oxygen as a function of depth, with pronounced maxima in bio-optical variables (e.g., Lizotte and Priscu 1992*a*; Vincent et al. 1998). Deep maxima of photosynthetic sulfur bacteria are also found in some Antarctic lakes, for example lakes Fryxell and Hoare (Lizotte and Priscu 1992*a*). In Lake A, peak concentrations of sulfur bacteria pigments were found between 20 m and 30 m, although anoxic conditions start at 14 m. The absence of measurable sulfide in waters above 32 m (J.A.E. Gibson et al., unpublished data) may explain the location of sulfur bacteria well below the oxycline.

Low irradiance attenuation in Lake A ice

The K_d(PAR) for lake ice measured in this study (0.32 m^{-1}) is within the range of ice values for Lake Vanda (0.19–0.67 m^{-1}; Howard-Williams et al. 1998), the clearest of the McMurdo Dry Valleys perennially ice-covered lakes. The dry climate of the Dry Valleys induces the formation of a highly scattering white ice layer at the ice surface as austral summer progresses, decreasing irradiance transmission through the ice (Howard-Williams et al.

Fig. 7. Spectral absorption coefficients of particles at selected depths in the water column of Lake A. Note the different scale for the 29 m spectra (right axis).

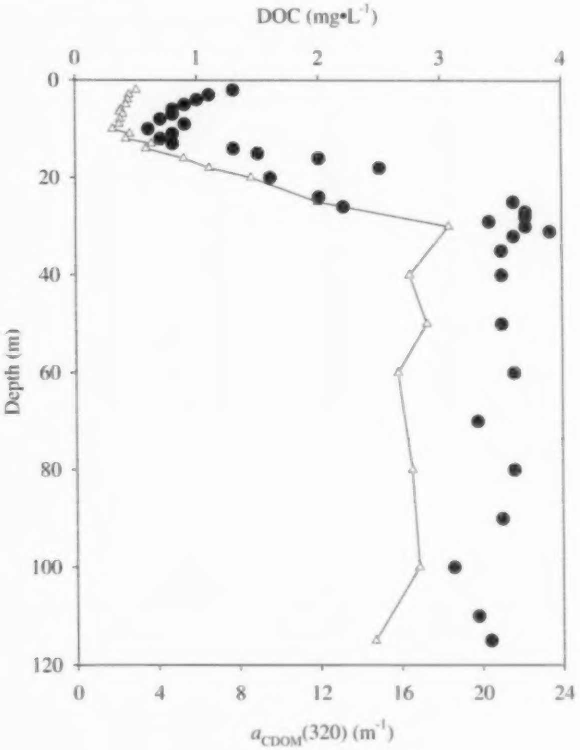


1998; Fritsen and Priscu 1999). Reduction of the transmittance through Antarctic lake ice also results from layers of wind-blown sediment present on top and inside the ice as well as numerous gas bubbles trapped in the ice (Wharton et al. 1993; Adams et al. 1998; Kepner et al. 2000). Sediment was present in the top metre of Lake A ice but as widely spaced aggregates that were unlikely to have a strong influence on the bulk radiative properties of the ice. However, these sediment aggregates are likely to cause melt lenses during summer and to modify bubble structure during freeze-down, thereby indirectly affecting local ice properties (Adams et al. 1998). Gas bubbles were observed although they appeared to be smaller and less numerous than reported for Antarctic lake ice (cf. Adams et al. 1998), presumably because of the lower O_2 and N_2 supersaturation in Lake A. Assuming that the sediment load had a negligible effect on ice buoyancy and given a density ratio of pure ice to water of 0.917 (Adams et al. 1998), the ice-cover density of 0.88 indicates an average air content of the ice cover of only 4%. The 12-cm-thick candled ice of Lake A therefore had a disproportionate impact on irradiance transmission because the remaining ice was so transparent.

The remarkably low K_d(UVR) in the ice relative to the water column of Lake A is likely to be the result of the dilute CDOM content of the ice. We have also measured reduced a_{CDOM} in the 2.3-m-thick ice of Char Lake (Cornwallis Island, 74°42′N); $a_{\mathrm{CDOM}}(320)$ in Char Lake ice on June 11, 1999, was 39 and 48% lower at 1 m and 1.5 m, respectively, than in the underlying water column (C. Belzile et al., unpublished data). Priscu et al. (1999*b*) reported the concentration of dissolved organic carbon in bottom accretion ice of Lake Bonney to be 58% of that of the water column, consistent with reduced CDOM in lake ice relative to water. Because of its high absorption in the UVR, CDOM is typically the main optical component controlling UVR attenuation in northern freshwaters (Laurion et al. 1997). The low a_{CDOM} in the ice thus allows Lake A ice to be relatively transparent to UVR despite elevated scattering. PAR attenuation is less affected by CDOM absorption owing to the exponential decrease of a_{CDOM} with increasing wavelength. Accordingly, K_d(PAR) in the ice was higher than in the water column, reflecting the higher scattering in the ice and the much lesser importance for PAR of the large CDOM differences between the ice and water.

Several mechanisms may explain the low a_{CDOM} in the ice. Firstly, freeze-outs of major ions, nutrients, and gases are known to occur during lake-ice formation and are more effective during periods of slow ice growth rate (Wharton et al. 1993; Adams et al. 1998). Ice accretion in Lake A is likely to be slow owing to the insulation provided by the thick ice and the relatively deep snow cover. Photochemical processes may contribute to a decrease of a_{CDOM} in the ice and may contribute to the fluorescence peaks indicative of small, simple molecules. Despite the short Arctic summer, the perennial nature of Lake A ice would allow relatively long exposure to UVR and the possibility of gradual photodegradation of DOC within the ice sheet. Finally, the sediment aggregates found in the top metre of the ice may be the site of microbial activity when liquid water is present, equivalent to the microbial consortium recently discovered in Antarctic lake ice (Priscu et al. 1998). Microbial degradation processes could accelerate the breakdown of CDOM. This biological activity may also result in autochthonous DOC production (Priscu et al. 1998), which could further explain spectral fluorescence peaks of small, simple molecules. In lakes of the Queen Maud Land (Antarctica), Kaup (1988) found situations where ice K_d(PAR) did not exceed that of

Fig. 8. Dissolved organic carbon concentrations (DOC; solid circles) and chromophoric dissolved organic matter absorption coefficients at 320 nm ($a_{CDOM}(320)$; open triangles) down the water column of Lake A.



the underlying water column. He noted that the ice crystals of the perennially ice-covered Lake Untersee can have diameters of 20 cm and more and can extend through the 3-m-thick ice. He postulated that these vertically oriented crystals act as light conductors, resulting in the very low K_d(PAR) for this type of ice. This situation may also apply to Lake A ice and the combination of low scattering and low absorption inside the ice crystals would allow relatively high UVR transmission through the ice.

Although the ice itself is relatively transparent to solar irradiance, the high albedo and K_d of the snow considerably reduced the irradiance reaching the water column. In early June, although solar irradiance was near its maximum, phytoplankton cells directly under the ice received at best 5 μmol photons·m^{-2}·s^{-1} of PAR. This is likely to cause severe light limitation. For example, even the highly shade-adapted phytoplankton in the McMurdo ice-covered lakes have light saturation values for photosynthesis of 10–30 μmol photons·m^{-2}·s^{-1} (Lizotte and Priscu 1992*b*).

Importance of CDOM in the water column

The attenuation coefficient of scalar PAR measured by Ludlam (1996) in the surface waters of Lake A was 0.304 m^{-1}, in good agreement with the value of 0.347 m^{-1} reported here. Water column K_d(PAR) and K_d(UVR) were low, although they were higher than those found, using the same radiometer, in perennially ice-covered lakes Vanda, Bonney, and Hoare in the McMurdo region (Vincent et al. 1998). This is consistent with the lower DOC concentrations recorded in these Antarctic lakes. UV attenuation in Lake A was similar to that measured in Lake Fryxell by Vincent et al. (1998), although DOC concentration is at least two times higher in the latter lake (McKnight et al. 1991; Vincent et al. 1998). It is likely that the DOC in these lakes is less colored than in Lake A, given their extremely barren catchments and the dominance by autochthonous processes in controlling their carbon dynamics. Approximately 5–10% of the ground around Lake A is covered with vegetation, mostly cushion plants (*Saxifraga oppositifolia*) but also some herbs and shrubs (including *Salix arctica* and *Dryas integrifolia*) (E. Lévesque, Université du Québec à Trois-Rivières, Trois-Rivières, Québec, unpublished data). These plants likely contribute to the allochthonous DOC input to the lake. As in Lake A, DOC concentrations increase with depth in most Antarctic perennially ice-covered lakes (e.g., from 1.3 to 3.9 mg·L^{-1} in Lake Hoare and from 3.3 to 30 mg·L^{-1} in Lake Fryxell; McKnight et al. 1991). McKnight et al. (1991) showed that the fulvic acid (FA) fraction of the DOC in lakes Hoare and Fryxell had similar elemental compositions, carbon distributions, and amino acid contents, indicating that the chemistry of these microbially derived FA is not strongly influenced by the chemical environment in the water column. However, the FA fraction represented only 16–20% of total DOC in these lakes. The very different fluorescence properties of CDOM observed through the water column of Lake A suggest that major differences in the composition of the DOM pool exist as a function of depth. The processes responsible for the presence in the suboxic and anoxic layers of CDOM with fluorescence characteristics typical of large and complex molecules remains to be elucidated. This fluorescent material may be remnant from the original DOC-containing ocean water that originally filled the basin or, more likely, may be the result of chemical (e.g., through sulfurisation by reaction with sulfide) or biological transformation of the simple material originating from the surface waters. These presumed modifications of the DOC pool are conspicuous in Lake A because of the highly stratified nature of the water column, but they are also likely to occur in other aquatic ecosystems. CDOM can be an important precursor of carbon substrates for heterotrophic growth and may help support mixotrophic phytoplankton during the long period of winter darkness (Priscu et al. 1999*a*).

In Lake A, UVR attenuation in the water column and ice would provide sufficient protection against UV damage to the photosynthetic sulfur bacteria growing below 13 m. The phytoplankton growing immediately under the ice are exposed to higher UVR fluxes, up to 6.3% of incident photoinhibiting solar irradiance under snow-free conditions (based on our snow-clearing experiment). Moreover, the ice surface artificially cleared of snow probably had a higher albedo because of the small residual amounts of snow trapped in the irregular ice surface and the influence of the snow at the edge of the cleared area. The air-filled candled ice was also likely more scattering than under melting conditions when liquid water ponding on the ice surface would substantially reduce the albedo. The irradiance transmission in natural

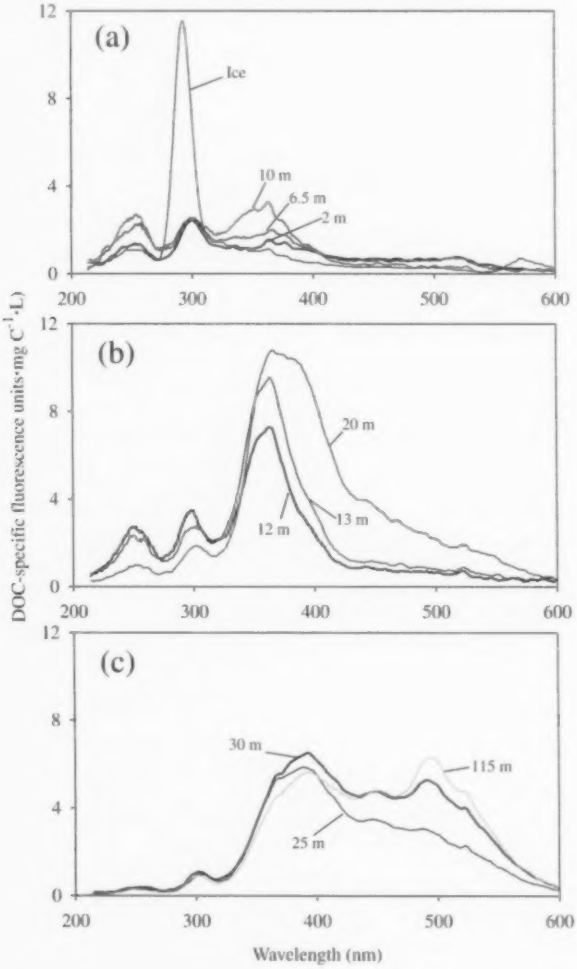


Fig. 9. Dissolved organic carbon specific synchronous fluorescence spectroscopy scans of chromophoric dissolved organic matter from the lake ice and selected depths in the water column.

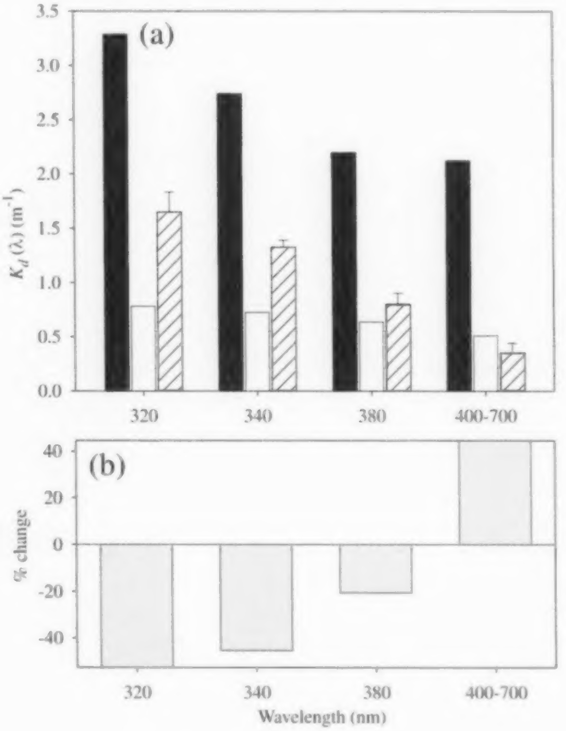


Fig. 10. (*a*) Snow (solid bars), ice (open bars), and water-column (hatched bars) attenuation coefficients for downwelling irradiance, $K_d(\lambda)$. Error bars for water-column $K_d(\lambda)$ are standard deviations for the means of five different profiles. (*b*) Percent change of $K_d(\lambda)$ in the ice relative to that in the water.

snow-free conditions is therefore likely to be higher than that measured here, unless significant "ice whitening" similar to that observed in Antarctic perennially ice-covered lakes (Fritsen and Priscu 1999) is occurring.

Climate change

Given the relative transparency of the ice cover, the opaque nature of the snow, and the strong seasonal variations in incident irradiance (complete darkness from mid-October until the end of February), most of the annual input of solar energy to the lake must be restricted to a brief period of the year. Simple model calculations based on K_d and assuming no change in surface albedo show that a 20% variation in snow depth would correspond to a similar percent change in the amount of PAR entering the lake (from $\%T = 0.50\%$ with $z_{\text{snow}} = 41$ cm to 0.41% and 0.60% with 49 cm and 22 cm of snow, respectively). However, the removal of snow over a 12-m^2 area increased %*T*(PAR) 13 times and would increase photoinhibiting UVR 16 times. Changes in the timing of the disappearance of snow cover would have a major impact on the annual radiation budget of the lake, with implications for stratification, mixing, and biological processes.

There is no statistical trend in the temperature or precipitation at Alert for the period 1951–1999 (C. Belzile et al., unpublished data). However, for the last 32 years of this record, there has been a significant warming trend in mean annual temperature (0.04°C per annum) and a highly significant decline in the number of freezing degree-days per annum (loss of 15 freezing degree-days per annum; Vincent et al. 2001). These most recent trends are likely to be related, at least in part, to the Arctic Oscillation, although they may also be amplified by anthropogenic forcing (Rigor et al. 2000).

There is considerable interannual variability in the Alert climate record. For example, snow depth at Alert at the end of the cold season ranged from 9 to 79 cm for the period 1949 to 1988 (Curtis et al. 1998), and a difference of 27 days was shown between the earliest (June 4th) and latest (July 1st) date of the onset of snowmelt (Table 1). Such variations in the thickness and duration of snow cover over the perennial ice of Lake A would translate into major interannual differences in the annual solar energy input to the lake and are likely to cause pronounced year-to-year differences in biological productivity. Despite this variability, however, the ice has remained on the lake on all years of direct or remote observation.

Changes greater than the interannual variability will accompany future warming trends in the region, as predicted by global models (Weller 1998). Relatively minor increases in air temperature beyond the 1998 maximum could cause the complete loss of ice cover of Lake A. Our optical results reported here show that such a change would completely alter the limnological characteristics of this High Arctic ecosystem.

Acknowledgments

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Retrospective patterns of differential mortality and common year-effects experienced by spring and summer chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River

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Abstract: We used spawner–recruit data to estimate the instantaneous differential mortality (μ) experienced by seven Snake River spring and summer chinook (*Oncorhynchus tshawytscha*) stocks relative to six lower Columbia River stocks. We applied 37 Ricker stock–recruit models to these data, incorporating different assumptions about measurement error, transport survival, intrinsic productivity, methods of estimating μ, and common year-effects that affect the survival of all stocks. Estimates of mean μ for the 12 best models ranged from 0.55 to 1.90 (mean of 1.09), implying that passage from Lower Granite Dam to John Day Dam reduced recruitment of 1970–1990 Snake River broods by an average of 42–85% (mean of 66%). Differential mortality was cyclical and moderately high in the 1970s brood years, low for 1980–1983, near average in 1984–1989, and high in 1990. Our empirical estimates of μ showed low bias and were between those produced by two mechanistic passage models. The best empirical models included common year-effects, which shifted from generally positive effects on 1952–1968 brood years to generally negative effects on 1970–1990 broods. Year-effects were not significantly correlated with two climate indices or with water travel time (the time that water takes to travel down the Columbia River).

Résumé : Des données sur les géniteurs et les recrues nous ont permis d'estimer la mortalité différentielle instantanée (μ) chez sept stocks de printemps et d'été du Saumon quinnat dans la rivière Snake, par comparaison à six stocks de l'aval du fleuve Columbia. Nous avons analysé ces données à l'aide de 37 modèles de stock–recrutement de Ricker qui incorporaient diverses présuppositions concernant les erreurs de mesure, la survie au transport, la productivité intrinsèque, les méthodes d'estimation de μ et les effets généraux de l'année sur la survie de tous ces stocks. Les estimations de μ pour les 12 meilleurs modèles variaient de 0,55 à 1,90 (moyenne de 1,09), ce qui indique que le passage du barrage Lower Granite à celui de John Day a réduit les cohortes de 1970–1990 de la rivière Snake d'en moyenne 42–85 % (moyenne globale de 66 %). La valeur de μ a varié de façon cyclique, modérément élevée chez les cohortes des années 1970, faible chez celles de 1980–1983, près de la normale chez celles de 1984–1989 et élevée chez celle de 1990. Nos estimés empiriques de μ montrent peu d'erreur et se situent entre ceux générés par deux modèles mécanistes de passage des poissons. Les meilleurs modèles empiriques incorporent les effets généraux de l'année, qui ont varié de généralement favorables pour les cohortes de 1952–1968 à généralement négatifs pour les cohortes de 1970–1990. Les effets de l'année ne sont pas en corrélation significative avec les deux indices climatiques, ni avec le temps requis par l'eau pour descendre le Columbia.

[Traduit par la Rédaction]

Introduction

Snake River spring and summer chinook salmon (*Oncorhynchus tshawytscha*) stocks have declined dramatically since the mid-1970s. They were listed as threatened under the Endangered Species Act in 1992 and reclassified as endangered in August 1994 on an emergency basis. The mid-1970s was a period of major changes in the anthropogenic and environmental conditions encountered by these stocks. The last of the Snake River dams were completed, hatchery production increased dramatically, there was a large increase in the number of fish transported in barges around the hydropower system, and there was a major shift in ocean conditions in the Northeast Pacific. Because all of these changes occurred around the same time, there are many hypotheses about the relative importance of these factors on the mortality of Snake River chinook salmon. These hypotheses were embodied in different management models, which had different underlying assumptions and consequently provided conflicting advice to managers about current and future actions that might best recover listed chinook stocks.

One of the key issues has been the magnitude and causes of systematic differences in spawner-to-recruit survival rates between spring and summer chinook stocks originating in Snake River sub-basins and stocks originating in sub-basins

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further downstream in the Columbia River system, as found in Schaller et al. (1999) (i.e., differences that remain after accounting for different productivity of stocks and for random effects in individual streams). We call these systematic differences "differential mortality". Because lower-river stocks pass through or around fewer dams, are not transported, have fewer hatchery influences, and possibly inhabit different areas of the Pacific Ocean than Snake River stocks, any of these factors could be explanations for observed differences in survival.

In an effort to resolve debates over this and other issues, the Plan for Analyzing and Testing Hypotheses (PATH) was initiated in 1995 (see Marmorek and Peters (2001) for a description of the PATH process). Within the PATH framework, agency and independent scientists rigorously evaluated evidence for and against explicit hypotheses about the distribution, cause, and magnitude of mortality over the life cycle of spring chinook salmon. They developed new data and analytical methods to address old questions. In particular, reconstructed time series of spawner and recruit data for spring chinook stocks of the Columbia River provided the opportunity to explore hypotheses about spatial and temporal patterns in mortality (Marmorek et al. 1998). Stock and recruitment data can provide a powerful basis for inferential hypothesis testing and parameter estimation regarding mortality experienced by juvenile chinook salmon during their down-river migration.

In this paper, we describe an analysis that takes advantage of this rich data set to explore retrospective patterns in the differential mortality experienced by chinook salmon populations from different regions of the Columbia River basin. Our goal was to estimate differential mortality by fitting stock and recruitment models to available data on recruitment and escapement and ancillary information. We exploit the fact that many of the dams along the Columbia and Snake rivers were completed at various times encompassed by the time series of available stock and recruitment data and that various populations are exposed to different numbers of dams, much in the spirit of the staircase experimental design method of Walters et al. (1989). An important set of our models rely on the hypothesis that Snake River and lower Columbia River spring and summer chinook salmon populations share a "common" mortality factor that can be used to partition total mortalities, as found in Schaller et al. (1999); Zabel and Williams (2000) contest that hypothesis and Schaller et al. (2000) respond to the contest. We refer the reader to those papers and to that of Marmorek et al. (1998) for background about why one might expect that similarities between Snake River and lower Columbia River chinook salmon populations could be exploited in order to characterize the remaining contrasting features of those populations.

We expand population modeling beyond the simple types of population models considered for Snake River and Columbia River chinook salmon in Schaller et al. (1999) and Botsford and Paulsen (2000). The primary model considered here is a generalization of the Ricker spawner and recruit model designed to accommodate a suite of factors thought to be important to the survival of the fish including year-specific factors for in-river passage mortality. Several alternative models can be structured by making alternative assumptions about terms in the primary model. This paper differs from others on the same salmon population (Schaller et al. 1999; Botsford and Paulsen 2000) in that we compare and test several alternative assumptions about the structure of a single general model and the types of errors that need to be accommodated in the modeling. We believe that our use of a general population model offers advantages over correlation analysis of salmon survival trends, as for example in Peterman et al. (1998) or in Botsford and Paulsen (2000), in that we are able to change assumptions about error sources and multiple factors simultaneously. A disadvantage to our approach is that even a general model is limited to only a subset of possible hypotheses about error structure and factors. Another disadvantage is that it can be too time consuming to explore all possible permutations of assumptions.

Methods

Spring and summer chinook salmon populations

We analyzed data for 13 populations of chinook salmon (Table 1) for which time series of spawner and recruitment information were available at the time of this analysis (Beamesderfer et al. 1997). Down-river stocks included those of the Wind, Klickitat, and Warm Springs rivers and three populations in the John Day sub-basin system (John Day Mainstem, John Day Middle Fork, and John Day North Fork). The seven up-river stocks were from the Minam (a tributary of the Grande Ronde), the Imnaha (a tributary of the Snake River), and Bear Valley, Marsh Creek, Sulphur Creek, Poverty Flat, and Johnson Creek (tributaries of the Salmon River). The stocks of the up-river sub-basins migrate past more dams than do the down-river stocks (Table 1). Recruitment refers to year-class abundance of each stock when they return to the Bonneville Dam on the lower Columbia River.

Estimates of recruitment are back-calculations based on expansion of spawner estimates to account for losses that occur during the migration of salmon from Bonneville Dam to their spawning ground. Spawner estimates are estimates of annual abundance of sexually mature salmon at their respective spawning grounds. More specifically, Beamesderfer et al. (1997) estimated numbers of spawners and returning recruits to the mouth of the Columbia River for the upstream and downstream salmon populations using spawning-ground surveys, age frequencies, mainstem and tributary harvest rates, and mainstem conversion rates for upstream passage of adults. They gathered this information from historical data sets, reports, and ongoing monitoring. A major goal of their analysis was to develop a consistent methodology for reconstructing spawner and recruit data across index stocks. As with any reconstructed data set of this spatial and temporal breadth, assumptions were necessary. Although these assumptions and data sources are thoroughly documented, they do introduce additional uncertainty.

A thorough discussion of the reconstruction methodology and data quality issues is beyond the scope and intent of this paper. However, we note that these data have been used in several recently published analyses (e.g., Schaller et al. 1999; Botsford and Pauslen 2000; Petrosky et al. 2001). Their quality and influence on model parameter estimates and analytical inferences has been debated both during the PATH process (Marmorek and Peters 2001) and in the subsequent published literature (response of Schaller et al. (2000) to Zabel and Williams (2000); Deriso 2001; Hinrichsen 2001). We direct interested readers to these papers and to the PATH literature for further elaboration of the strengths and potential weaknesses of these data. In particular, Schaller et al. (1999) provides an excellent overview of the rationale and methods used by Beamesderfer et al. (1997). The full analysis of Beamesderfer et

Table 1. Summary information on the 13 chinook populations analyzed in this study.

Region	Sub-basin	Brood years of paired spawner–recruit data	Number of mainstem dams below sub-basin
Lower river	1. Wind	1973–1990	1
	2. Klickitat	1966–1990	1
	3. Warm Springs	1969–1990	2
	4. John Day Mainstem	1959–1990	3
	5. John Day Middle Fork	1959–1990	3
	6. John Day North Fork	1959–1990	3
Snake River	7. Imnaha	1952–1990	8
	8. Minam	1954–1990	8
	9. Bear Valley	1957–1990	8
	10. Marsh Creek	1957–1990	8
	11. Sulphur Creek	1957–1990	8
	12. Poverty Flat	1957–1990	8
	13. Johnson Creek	1957–1990	8

al. (1997) and the PATH literature are available at http://www.efw.bpa.gov/Environment/PATH/.

Population models

We focus on stock and recruitment models that assume that survival rates of chinook from rivers of the Snake and Columbia systems share many similar aspects. In particular, ocean mortality rates are assumed to share many common attributes across stocks from different streams. By making this assumption, differential mortality between up-river and down-river stocks can be attributed to differences in their in-river passage. To accommodate this assumption, our general model contains an optional year-effect component to reflect common factors affecting survival of all stocks.

The general model structure is based on a Ricker-type spawner–recruitment model that explicitly accounts for measurement error:

$$(1) \qquad y_{t,i} = x_{t,i} + a_{t,i} - b_i e^{x_{t,i}} - m_{t,i} + \varepsilon_{t,i}$$

$$(1a) \qquad \ln(S_{t,i}) = x_{t,i} + \varepsilon'_{t,i}$$

for which $y_{t,i}$ is the logarithm of recruitment; $R_{t,i}$ is the Columbia River "observed" recruitment originating from spawning in year t and river sub-basin i (number of fish); $S_{t,i}$ is the "observed" spawning in year t and river sub-basin i (number of fish); $x_{t,i}$ is the logarithm of "true" spawning; $a_{t,i}$ is the Ricker a parameter which depends on year and sub-basin (per year); b_i is the Ricker b parameter (1/number of fish); $m_{t,i}$ is the total passage mortality (direct dam mortality + differential mortality), which depends on year and sub-basin (per year); $\varepsilon_{t,i}$ is a normally distributed mixed process error and recruitment measurement error term $N(0,\sigma_\varepsilon^2)$ (per year); $\varepsilon'_{t,i}$ is a normally distributed spawner enumeration measurement error term $N(0,\sigma_{\varepsilon'}^2)$ (per year); t is the year; and i is the sub-basin.

Chinook salmon may return to spawn at ages 3, 4, or 5, but our model does not contain separate mortality terms for each age-class of a given brood. Instead, we assumed a constant post-age-4 ocean survival. Interannual variation in marine survival is confined to the first 2 years of life in the estuarine and ocean environment. In their final years at sea, ocean mortality for chinook salmon is probably lower and not likely to induce large systematic variation in total ocean mortality (Schaller et al. 1999).

Density-independent mortality

Equation 1 combines all non-dam, density-independent mortality sources into a single parameter $a_{t,i}$, except for the additive process error $\varepsilon_{t,i}$. Thus, the a parameter contains a sum of egg-to-fry, fry-to-smolt, and smolt-to-adult density-independent mortality. The density-dependent parameter b is chosen to be area specific to reflect the different carrying capacities of different areas. Typically, estimates of the a and b coefficients are confounded so we did not attempt to model temporal changes in carrying capacity explicitly.

We added structure for the a parameters in three alternative ways:

$$(2) \qquad a_{t,i} = a + \delta_t$$

$$(3) \qquad a_{t,i} = a_i + \delta_t$$

$$(4) \qquad a_{t,i} = a_i + \delta_{t,\text{region}}$$

where for each alternative the parameter a is the Ricker a parameter, i is the sub-basin (e.g., Imnaha), and "region" refers to either the up-river or the down-river sub-basins. In eq. 2, the model assumes the same Ricker a value for all stocks except for Wind because it is an introduced stock (Schaller et al. 1999). In eq. 3, the model allows the Ricker a parameter to vary for each stock. We included the year-effect parameter δ_t to allow for year-effects common to all stocks; this would include major ocean mortality changes that affect the survival of chinook salmon during the first 2 years of ocean life, as well as regional changes in terrestrial climate that affect all stocks. Above-average climate conditions have $\delta_t > 0$, whereas below-average conditions have $\delta_t < 0$. Using either eq. 2 or eq. 3 as part of the overall model in eq. 1 requires the assumptions that (*i*) year-to-year variations in climate that effect the ocean survival of all stocks will be picked up by the year-effect δ_t; (*ii*) random variations among stocks in ocean survival (owing to, for example, different ocean distributions or timing of ocean entry) will be assigned to the term $\varepsilon_{t,i}$ in eq. 1, which picks up any unexplained natural variation in survival during a fishes life until recruitment as well as recruitment measurement error; and (*iii*) variations among stocks in ocean survival are not systematic differences between up-river and lower-river stocks as regional stock groups.

To examine the sensitivity of the model to the third assumption, we added eq. 4, a generalization of eq. 3 that allows year-effects to differ between the up-river and lower-river stocks. When eq. 4 is implemented, an additional sum-of-squares (SSQ) term is needed in the estimation procedure to characterize the correlation between the year-effects in the two stock groups. If the within-region differences among stocks in year-effects are as large as the among-region differences, then these random effects will be assigned to the residual variation term $\varepsilon_{t,i}$. In such a case, there is no confounding of differential mortality estimates. However, in the special case where there are systematic differences between the year-effects of up-river stocks and those of lower-river stocks (i.e., differences between stock groups are significantly greater than those within each stock group), then there is confounding of the parameter estimates for the up-river differential mortality and the region year-effects.

Eliminating spawner measurement error ($\varepsilon'_{t,i}$ in eq. 1*a*), combining eqs. 1, 1*a*, and 3, and rearranging terms generates the following equation for our primary model:

$$(4a)\qquad \ln(R_{t,i}/S_{t,i}) = (a_i + \delta_t - m_{t,i}) - b_i S_{t,i} + \varepsilon_{t,i}$$

Equation 4*a* contains the following parameters that need to be estimated: δ_t, a_i, b_i, $m_{t,i}$, and the "true" spawning population abundances ($x_{t,i}$ in eq. 1*a*). Equation 4*a* is identical in structure to the multiple regression model commonly used to estimate the parameters of the Ricker model (Ricker 1975). The four major differences between our models and the standard Ricker model are as follows: (*i*) the inclusion of spawning enumeration measurement errors as estimated parameters; (*ii*) the specific independent variables used to explain variation in $\ln(R_{t,i}/S_{t,i})$ (i.e., right side of eq. 4*a*); (*iii*) the use of maximum likelihood estimation (MLE) procedures; and (*iv*) the grouping of stocks and years for the purposes of parameter estimation. Exponentiating both sides of eq. 4*a* generates the familiar Ricker equation plus two additional terms for the year and differential mortality effects:

$$(4b)\qquad R = Se^{a_i - b_i S_{t,i} + \varepsilon_{t,i} + \delta_t - m_{t,i}}$$

Exponentiating δ_t and $m_{t,i}$ expresses these parameters as fractional factors which in any given year can increase or decrease the recruitment from that expected by the Ricker parameters alone:

$$(4c)\qquad R = S(e^{a_i - b_i S_{t,i} + \varepsilon_{t,i}})(e^{\delta_t})(e^{-m_{t,i}})$$

Differential mortality (μ)

The emphasis of this study was the estimation of the differential mortality experienced by Snake River chinook populations from their sub-basins up to the John Day Dam for each brood year from 1970 to 1990. To do this, we used four alternative approaches to parameterizing *m*. The first approach uses a two-level parameterization scheme in which we separated dam mortality into two categories, as indicated by the Xs and Ys in Table 2 and referred to below as X-type and Y-type dam mortality. We assume that $m_{t,i}$ in eq. 1 is computed by

$$(5)\qquad m_{t,i} = X\cdot n + \mu_t$$

where *n* is the number of X-type dams in Table 2 (John Day to Bonneville after 1970), *X* is the dam passage mortality associated with each X-type dam, and μ_t is the differential mortality from the Snake River sub-basins to John Day Dam (Y-type dams in Table 2), expressed as an instantaneous mortality rate for brood years $t \geq 1970$. Years shown in Table 2 are based on the year of initial service of each dam, lagged by 2 years to standardize to brood year (Snake River spring and summer chinook migrate down river as smolts 2 years after they are spawned). The first level of parameterization (number of Xs in each row of Table 2) treats mortality as a process proportional to the number of dams passed by juvenile salmon during their transit to the ocean, excluding those dams and (or) populations treated in the second level. At the second level of parameterization (Ys in Table 2), the differential mortality experienced by upstream stocks is estimated by μ_t, which we assume is ≥0. The μ term is a "net" effect mortality estimate because it reflects the overall impacts of dam passage over the complete life cycle. This includes direct losses owing to trauma at the point of dam passage, increased "natural" mortality (e.g., predation) resulting from longer smolt residence time in dam reservoirs, latent mortality owing to the weakened condition of smolts, and the benefits or detriments of transportation by barge for some Snake River smolts down river to below the Bonneville dam.

Mortality in any given year for any given population is obtained in Table 2 by adding the number of X dams encountered by that stock (*n* in eq. 5) and multiplying that by a mortality rate per dam, plus a second-level annual term for μ_t provided that at least one Y dam is encountered by that stock. The Warm Springs stock, for example, which currently passes through only Bonneville and Dalles dams, would currently have $n = 2$ (Bonneville and Dalles dams) and $\mu_t = 0$. Johnson Creek, however, which passes through all eight dams, would have $n = 3$ (Bonneville, Dalles, and John Day) and an estimate of μ_t over five dams (McNary, Ice Harbor, Lower Monument, Little Goose, and Lower Granite).

The weakness of the first parameterization approach is that all per-dam mortality rates for the X dams are the same; there is no variation among dams or years. In the second parameterization approach, we address this weakness by using time-series estimates of total direct passage mortality ($M_{t,i}$) from the CRiSP (Columbia River Salmon Passage; Anderson et al. 1996) and FLUSH (Fish Leaving Under Several Hypotheses; Wilson 1994) passage models to create more flexible estimates of mortality for the dams and years with Xs in Table 2. The term $M_{t,i}$ is the total direct passage mortality from Lower Granite Dam (the first dam encountered by Snake River fish) to Bonneville Dam (the last dam encountered before fish reach the ocean); it is a weighted average of the dam and reservoir mortality experienced by nontransported fish and the barge mortality experienced by transported fish. The approach is to replace ($X\cdot n$) in eq. 5 by passage mortality proportional to that generated by the CRiSP or FLUSH models for the X dams only:

$$(6)\qquad m_{t,i} = qM_{t,i} + \mu_t$$

where *q* is a proportionality constant (estimated in the MLE procedure) to be multiplied by the passage mortality from CRiSP and FLUSH for X-type dams. Including a proportionality constant allows the estimation algorithm to mimic the pattern of mortality changes in CRiSP–FLUSH, scaling up or down as required, without constraining the estimated mortality to be the actual value predicted by the passage models. The CRiSP–FLUSH model estimates include both dam-induced effects within the river system and a background level of "natural" mortality within the river passage. Some natural mortality between John Day Dam and Lower Granite Reservoir would be expected even without any dams along the Columbia River (0–20%; Toole et al. 1996). Therefore, a reduction of the CRiSP–FLUSH estimated mortalities by 0.0 to 0.2 would be needed to make them strictly comparable to the μ_t estimates, which only consider the differential mortality caused by downstream passage.

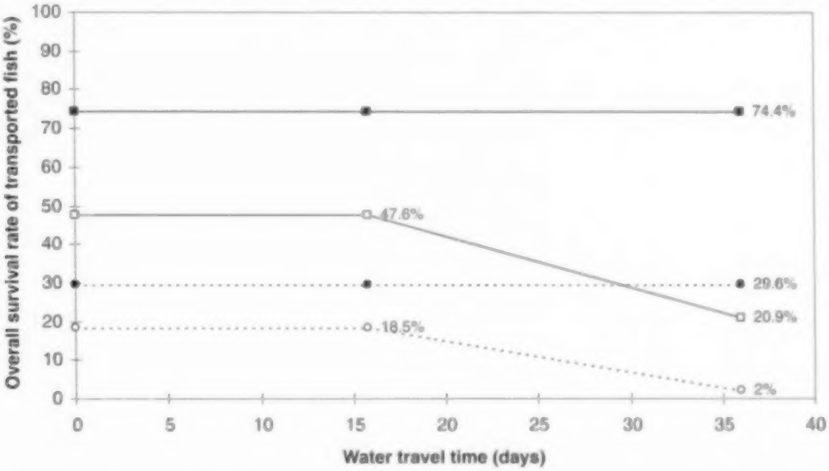
The third approach is to eliminate μ_t from eq. 6 and estimate $m_{t,i}$ for all of the dams passed by a given stock using estimates from passage and transportation models, either with or without the proportionately constant *q*. Two transport survival assumptions were applied to CRiSP and FLUSH, which led to four estimates of total direct passage mortality (Fig. 1). The transport survival assumptions are based on the ratio of survival of transported fish to nontransported (in-river) fish (transport–control ratio or T:C) in selected years of experiments, multiplied by the survival rate of in-river fish estimated by each passage model for those years. Transport survival therefore reflects smolt survival in the barge or truck, adjusted by the inferred relative survivals of transported and in-river fish after the last dam. Transport model 1 (T1) assumes that survival varies with water travel time (WTT, the average number of days that it takes a particle of water to get from the head of Lower Granite Reservoir to below Bonneville Dam during the spring migration period). The slope of the relationship is anchored at the high end by transport survival estimates using T:C values of 1.0:1 in 1986 (a high-flow, low-WTT year) and at the low end by trans-

Table 2. Types of passage mortality estimates.

	Dams							
Brood year(s)	BON	TDD	JDA	McN	IHR	LOMO	LGS	LGR
1952–1954	X			X				
1955–1958	X	X		X				
1959–1965	X	X		X	X			
1966	X	X	X	X	X			
1967	X	X	X	X	X	X		
1968–1969	X	X	X	X	X	X	X	
1970–1972	X	X	X	Y	Y	Y	Y	
1973–present	X	X	X	Y	Y	Y	Y	Y

Note: For the simplest models, X = fixed estimate of mortality/dam; Y = annually varying estimates of mortality resulting from passage through five dams; BON, Bonneville; TDD, Dalles; JDA, John Day; McN, McNary; IHR, Ice Harbor; LOMO, Lower Monumental; LGS, Little Goose; LGR, Lower Granite). More complex models replace the Xs with estimates either proportional or equal to CRiSP–FLUSH mortality estimates.

Fig. 1. Comparison of CRiSP (Columbia River Salmon Passage) and FLUSH (Fish Leaving Under Several Hypotheses) transport model survival assumptions. Model T1 assumes that transport survival decreases with water travel time, whereas model T2 assumes constant survival. FLUSH T2, ●; FLUSH T1, ○; CRiSP T2, ■; CRiSP T1, □.



port survivals using a T:C value of 3.0:1 in 1977 (a low-flow, high-WTT year). Transport model 2 (T2) assumes fixed survival, calculated based on a T:C of 1.6:1 for 1986 (this represents a point estimate for release to return at Little Goose Dam, the lower T:C in 1986 for T1 reflects survival to the spawning grounds). For both sets of assumptions, FLUSH clearly estimated much lower transport survival than CRiSP (Fig. 1). Revised versions of CRiSP, FLUSH, and the transportation models have been distributed since this analysis was completed (Peters and Marmorek 2001). However, the same general patterns still hold: CRiSP estimates of transport survival rate are generally much higher than FLUSH estimates.

The fourth approach again uses the two-level approach described in eq. 5 except that μ_t is assumed to be proportional to WTT. WTT is a candidate variable because longer travel times expose smolts to reservoir predators for longer periods and cause fish to experience more delays when passing dams. Transported fish may also reach the point of transport in poorer condition in low runoff years (high WTT), consistent with the general pattern in model T1 (Fig. 1).

Likelihood function and bias correction procedure

A set of 37 spawner–recruit models were developed, each representing a different combination of assumptions about spawner measurement error, parameterization of Ricker *a*, parameterization of *m*, and the commonality of year-effects (Table 3). We calculated likelihoods for each model using a likelihood function made up of two parts: the normal errors for the usual error term in a Ricker model $\varepsilon_{t,i}$ and the normal errors for the spawner measurement error $\varepsilon'_{t,i}$. MLE estimates for all parameters are obtained by minimizing the negative log-likelihood function, which reduces to minimizing the following sum-of-squares:

$$\text{(7)} \qquad \text{SSQ} = \sum \varepsilon_{t,i}^{\;2} + \lambda_{\varepsilon'} \sum \varepsilon'^{\;2}_{t,i}$$

where the variance ratio $\lambda_{\varepsilon'} = \sigma^2_{\varepsilon} / \sigma^2_{\varepsilon'}$ is specified a priori. Spawner-measurement error was estimated to have a coefficient of variation of 24%, based on a comparison of redd counts to weir counts in the Lemhi River (C. Petrosky, Idaho Department of Fish and Game, 600 S. Walnut, Boise, ID 83707, personal communication). Preliminary analyses showed that process error had a variance slightly larger than the measurement error variance and $\lambda_{\varepsilon'}$ was set equal to 1.5 in models for which both error terms were estimated. The likelihood function for the model that includes regional year-effects (i.e., eq. 1 with eq. 4 for $a_{t,i}$) contains an additional SSQ term:

Table 3. Results of applying 37 different models to stock and recruitment data.

Model number	Spawning measure error?	Different *a*?	Distinguishing features	Total sums of squares
1*	N	Y	Eq. 5 total passage mortality (*m*)	111.88
2	Y	Y	Eq. 5 total passage mortality (*m*)	92.14
3*	N	N	Eq. 5 total passage mortality (*m*)	120.07
4	Y	N	Eq. 5 total passage mortality (*m*)	96.3
5*	N	Y	X-type dam mortality proportional to CRiSP T1	111.49
6*	N	Y	X-type dam mortality proportional to CRiSP T2	111.47
7	N	Y	X-type dam mortality proportional to FLUSH T1	113.09
8	N	Y	X-type dam mortality proportional to FLUSH T2	113.09
9	N	Y	*m* passage mortality rate proportional to CRiSP T1	149.27
10	N	Y	*m* passage mortality rate proportional to CRiSP T2	157.06
11*	N	Y	*m* passage mortality rate proportional to FLUSH T1	141.49
12	N	Y	*m* passage mortality rate proportional to FLUSH T2	152.67
13	N	Y	*m* passage mortality rates = CRiSP T1 values	153.19
14	N	Y	*m* passage mortality rates = CRiSP T2 values	179.72
15	N	Y	*m* passage mortality rates = FLUSH T1 values	155.02
16	N	Y	*m* passage mortality rates = FLUSH T2 values	164.07
17	N	Y	$m = X \cdot$(total number of dams passed)	149.99
18*	N	Y	(Same as No. 13 CRiSP T1), except exclude BY 1971	147.62
19	N	Y	(Same as No. 14 CRiSP T2), except exclude BY 1971	174.02
20*	N	Y	(Same as No. 15 FLUSH T1), except exclude BY 1971	141.95
21*	N	Y	(Same as No. 16 FLUSH T2), except exclude BY 1971	146.86
22	N	Y	Sub-basin year-effects; *m* as in No. 1; λ(basin) = 0.01	107.12
23	N	Y	Sub-basin year-effects; *m* as in No. 1; λ(basin) = 1.0	108.64
24	N	Y	Sub-basin year-effects; *m* as in No. 13; λ(basin) = 0.01	106.51
25	N	Y	Sub-basin year-effects; *m* as in No. 13; λ(basin) = 1.0	118.62
26	N	Y	Sub-basin year-effects; *m* as in No. 14; λ(basin) = 1.0	126.42
27	N	Y	Sub-basin year-effects; *m* as in No. 15; λ(basin) = 1.0	119.32
28	N	Y	Sub-basin year-effects; *m* as in No. 16; λ(basin) = 1.0	121.62
29	N	Y	$m = X \cdot$(total number of dams passed); no year-effect	299.48
30	N	Y	No year-effect; *m* as in No. 11, FLUSH T1	289.89
31*	N	N	*m* passage mortality rate proportional to CRiSP T1	154.17
32	N	N	*m* passage mortality rate proportional to CRiSP T2	167.17
33*	N	N	*m* passage mortality rate proportional to FLUSH T1	149.53
34	N	N	*m* passage mortality rate proportional to FLUSH T2	158.23
35	N	N	$m = X \cdot$(total number of dams passed)	158.56
36*	N	N	μ passage mortality rate proportional to WTT	145.82
37*	N	Y	μ passage mortality rate proportional to WTT	136.28
			Average across all models	144.59
			Median value	145.82

Note: Top models (* after model number) have AIC and BIC values below the median for all models. WTT is water travel time. Equation 1 applies to defined by eqs. 7 and 7*a*. Number of parameters are obtained by counting parameters in eq. 1, configured with the appropriate optional equations listed in eqs. 7 and 8. Average μ is the average of the estimates in eq. 5 for brood years 1970–1990. The average Ricker *a* parameter is obtained by averaging Under Several hypotheses; Y, yes; N, no.

$$(7a)\qquad \mathrm{SSQ} = \sum \varepsilon_{t,i}{}^{2} + \lambda_{\varepsilon'} \sum \varepsilon'_{t,i}{}^{2} + \lambda_{\mathrm{region}} \sum (\delta_{t,\mathrm{region1}} - \delta_{t,\mathrm{region2}})^{2}$$

in which $\lambda_{\mathrm{region}}$ is the variance ratio (similar to $\lambda_{\varepsilon'}$), $\delta_{t,\mathrm{region1}}$ is the year-effect for lower-river stocks and $\delta_{t,\mathrm{region2}}$ is the year-effect for up-river stocks. The variance ratio term $\lambda_{\mathrm{region}}$ was set to 1.0 because we had no better estimate.

The MLE estimates were obtained by application of a Marquardt nonlinear minimization routine (Draper and Smith 1966). We applied a Monte Carlo bootstrap procedure (Efron 1979, 1981) to the MLEs to produce median unbiased estimates. The bootstrap method is identical to the one described in Deriso et al. (1985) in which we sample, with replacement, the residuals from the original model fitting, generate pseudo-observed data, and then fit the model to pseudo-observed data, repeating this process 100 times. Median estimates from the bootstrap trials provide an estimate of bias for the original MLEs. The bias appears to be rather minor in the results (usually less than 10% of the estimated quantity). Therefore, a first-order procedure such as the bootstrap procedure appears to be a reasonable approach in this case, although the method may not work well with other data sets that exhibit larger bias (C. Walters, 2204 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, personal communication; J. Collie, University of Rhode Island, Narragansett, RI 0882-1197, personal communication). All model results reported here were corrected for bias by subtracting the estimated bias from the MLE estimates.

Number of parameters estimated	Number of likelihood components	Akaike information criterion (AIC)	Bayesian information criterion (BIC)	Average μ	Average Ricker *a* parameter
86	406	800.7	1145.2	1.44	2.65
492	812	1520.9	3833.0	1.26	2.45
75	406	807.4	1107.8	0.82	1.84
492	823	1553.4	3872.2	0.81	1.84
86	406	799.3	1143.8	1.07	2.12
86	406	799.2	1143.7	1.07	2.13
86	406	805.0	1149.6	1.02	1.97
86	406	805.0	1149.6	1.02	1.97
65	406	875.7	1136.1	0.59	1.95
65	406	896.4	1156.8	0.02	1.53
65	406	854.0	1114.4	0.99	2.03
65	406	884.9	1145.3	0.54	1.81
64	406	884.3	1140.7	1.00	2.26
64	406	949.1	1205.5	0.48	2.04
64	406	889.1	1145.5	1.90	2.51
64	406	912.1	1168.5	1.40	2.29
65	406	877.7	1138.1	1.44	2.68
63	393	856.3	1106.6	1.00	2.24
63	393	920.9	1171.3	0.48	2.02
63	393	840.9	1091.2	1.90	2.50
63	393	854.2	1104.6	1.40	2.27
118	438	861.9	1343.6	1.43	2.65
118	438	868.1	1349.8	1.44	2.65
96	438	815.4	1207.3	1.00	2.35
96	438	862.6	1254.5	1.00	2.32
96	438	890.5	1282.4	0.48	2.16
96	438	865.2	1257.1	1.90	2.48
96	438	873.6	1265.4	1.40	2.33
27	406	1082.4	1190.6	1.88	3.04
27	406	1069.2	1177.4	1.32	2.02
54	406	866.8	1083.2	0.55	1.89
54	406	899.7	1116.1	0.14	1.63
54	406	854.4	1070.8	0.71	1.85
54	406	877.4	1093.7	0.53	1.77
54	406	878.2	1094.6	0.57	1.94
55	406	846.2	1066.6	0.79	1.78
66	406	840.8	1105.2	1.34	2.52
94.14	432.89	909.16	1306.16	1.03	2.17
65	406	868.1	1145.3	1.00	2.13

all models. Entries in columns 2, 3, and 4 are variations on eq. 1 created using eqs. 1*a*, 2, 3, 4, 5, and 6. The total sums of squares is the sum of squares
above, and counting numbers of stocks and years of data in Table 1 for the particular model. Number of likelihood components are the number of terms
estimates across the seven sub-basin stocks in the Snake River region. BY, brood year; CRiSP, Columbia River Salmon Passage; FLUSH, Fish Leaving

Detailed testing over a range of dam mortalities and model structures indicated that the lowest bias models included estimates of X-dam mortality and stock-specific Ricker *a* values and assumed no spawner measurement error.

Ranking alternative models

We used two criteria for assessing the relative fits of each model to data: the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) (Akaike 1973; Kass and Raftery 1994). Better model fits correspond to lower AIC and BIC scores. The AIC, given by the equation

$$\text{AIC} = -2\ln(\text{likelihood}) + 2p \tag{8}$$

and the BIC, given by the equation

$$\text{BIC} = -2\ln(\text{likelihood}) + p\ln(k) \tag{9}$$

are both based on asymptotic properties of the likelihood function (p is the number of parameters estimated and k is the number of "observations", where we count observation number as the number of SSQ components). Both the AIC and BIC use twice the log-likelihood, which is asymptotically a χ^2 statistic. Therefore, both statistics are also related to asymptotic likelihood ratio tests that use classical hypothesis testing to test nested models (Mood et al. 1974). Both the AIC and, to a much greater extent, the BIC correspond to a very small rejection criterion (probabilities below 0.005) for alternative nested models with 21 or more additional parameters in the larger model (as we have in this study). That is, neither the AIC nor BIC criteria will reject a simple model in favor of a more complex model unless there is a significant improvement in SSQ ($p < 0.005$).

There are differing perspectives on which criterion should be used to select models (Kass and Raftery 1994). From a Bayesian perspective, Gelman et al. (1996) argue against model selection altogether, as the alternative models represent alternative hypotheses that should not be discarded. Instead, the model should be general enough to contain alternatives as special case solutions to allow calculation of posterior probabilities that reflect the relative credibility of alternative hypotheses. A reasonable compromise would be only to reject models that are grossly less supported by AIC and BIC but reserve judgement on the remaining ones.

Results

Relative fits of models to data

Relative fits of the 37 spawner–recruitment (*S–R*) models to the spring and summer chinook spawner–recruitment data series are shown in Table 3. The best (lowest) AIC scores occurred for models where μ was estimated each year (models 1, 3, and 5–8). Among those models, comparable AIC values were produced by models that parameterized X-dam mortality as a constant per-dam mortality and by models in which X-dam mortality was proportional to passage model estimates. The best (lowest) BIC scores occurred for models with fewer parameters (particularly models 33 and 36), although these models still included year-effect parameters. Simple parameterizations for μ were favored by the BIC criterion, either as μ proportional to WTT, as in model 36, or with total differential mortality *m* proportional to passage model values from CRiSP or FLUSH (models 31–34).

Based on the results in Table 3, we identified a set of 12 "top" models for which both the AIC and BIC were below the median for all 37 models. Top models were 1, 3, 5, 6, 11, 18, 20, 21, 31, 33, 36, and 37 from Table 3. All top models included a common year-effect and excluded spawner measurement error. Both assumptions about commonality of the Ricker *a* parameter were represented in the set of top models, as were all four approaches to estimating *m*. Parameter estimates for the top models support a wide range of alternative hypotheses about the magnitude of the up-river net differential mortality μ and Ricker *a* parameters. Average μ for the top models ranged from 0.55 to 1.90 (mean of 1.09), which corresponds to a range of 42–85% ($100(1 - e^{-\mu})$) mortality owing to downstream passage from Lower Granite to John Day dams, over the entire life cycle (mean of 66%). Average Ricker *a* values of these models ranged from 1.78 to 2.65 (mean of 1.92). The range in average production index ($a - \mu$) for these models was smaller, from 0.60 to 1.34 (mean of 1.06). The smaller range in average production reflected the correlation between estimates of μ and *a*, which was also present in the bootstrap simulations done for models 1 and 3. Higher differential mortality estimates required higher production values to match observed patterns in spawner–recruit data.

Temporal patterns in differential mortality, total passage mortality, and common year-effects

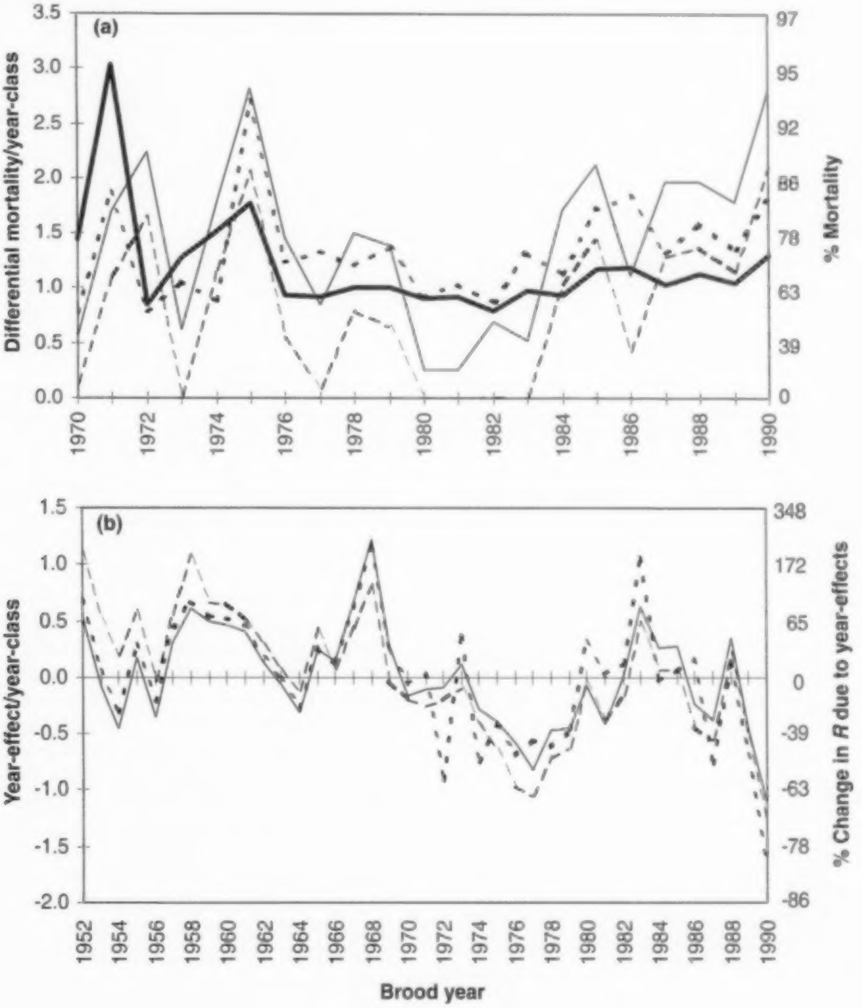
Time trends in μ and year-effects for a subset of three of the models are shown in Fig. 2. These models were typical of ones for which both a year-effect and yearly μ parameter were estimated. Models 1 and 4 used the first parameterization of differential mortality given above (i.e., eq. 5; constant mortality per project) but used different assumptions about inclusion of spawner measurement error and differences in Ricker *a* parameters among stocks. Model 1 did not include spawner measurement error and estimated a different Ricker *a* parameter for each stock. Model 4 included measurement error and estimated a single *a* parameter for all stocks. Overall, models 1 and 4 provided upper and lower bounds, respectively, on the μ values estimated by models 1 to 8 in Table 3, where models 5–8 used X-dam mortality proportional to the passage model estimates. The final model, number 37 of Table 3, was included in Fig. 2 because of its low BIC score and because it contained a simplified passage model: μ proportional to WTT. This model had a slightly higher BIC score than that of model 36 but was chosen because it included different Ricker *a* parameter values (shown in simulation tests to perform more accurately).

All three *S–R* models gave similar estimates of time trends both in μ (differential mortality from Snake River sub-basins to John Day Dam) and in δ_t (year-effect parameter) (Fig. 2). The time trend in μ was one of a cyclical high to moderate mortality throughout the 1970s followed by a 4-year period of low mortality (1980–1983), then a return to a stable but slightly cyclical mortality through the latter half of the 1980s, and an upward spike in 1990 (Fig. 2*a*). Figure 2*a* shows the average of the four CRISP–FLUSH and T1–T2 differential mortality estimates (μ), whereas Fig. 3 shows each of these four models' estimates of μ separately. Average passage model estimates of μ generally passed through the μ estimates of the four *S–R* models with three notable exceptions: (*i*) the spiked mortality indicated by the passage models for brood year 1971 was not present in any of the *S–R* models (survival trends show that brood year 1972 was the poor year, not 1971, especially for the Bear Valley, Sulphur Creek, Poverty Flats, and Johnson Flats populations); (*ii*) the mortality indicated by the passage models for brood years 1980–1983 did not show the precipitous reduction in mortality (increase in survival) indicated in all *S–R* models; and (*iii*) the increased mortality in all eight models in 1990 was above the average passage model. A previous examination of the 4-year high survival result in 1980–1983 showed that the reduction in mortality for the up-river populations was due to both real increases in recruitment and decreases in spawning population. The decrease in spawning populations was also observed on the lower-river populations, but they did not experience the increase in recruitment that was seen in up-river populations. The four passage models showed substantial differences in estimated μ. Though the CRiSP T2 passage–transportation model also showed low μ (high survival) during 1980–1983, it did not show the subsequent increasing mortality indicated by the *S–R* models (Fig. 3). A moderate long-term cycle was present for estimated year-effects (Fig. 2*b*), indicating a shift in climate mortality regimes from a generally high positive anomaly sequence for the 1952–1968 brood years followed by generally negative anomalies for the 1970–1989 brood years.

Year-effects

There was strong support for inclusion of year-effects in

Fig. 2. (*a*) Estimates of differential mortality (μ) above John Day Dam by brood year for three stock–recruitment models (numbers 1, 4, and 37 in Table 3) and the average of estimates produced by four passage and transport models. The second *y* axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$). (*b*) Year-effect (δ) estimates for the same three stock–recruit models (year-effects were not estimated by passage and transport models). The second *y* axis converts δ to an estimated percent change in recruitment ($100(e^{-\delta} - 1)$). Model 1, thin solid line; model 2, thin broken line; model 37, thick broken line; average passage model (Fig. 2*a* only), thick solid line.



the models, as seen by the high AIC and BIC scores (poorer fits) for models 29 and 30 in which no year-effect was included. Regional year-effects were investigated in models 22 to 28. BIC scores for those regional models were substantially poorer than models without region-specific year-effects (models 1 and 13–16 in Table 3). AIC scores were poorer for models 22 and 23 than for model 1, one of the better empirical models. However, the CRiSP- and FLUSH-based models showed lower AIC values when region-specific year-effects were included (models 24–28 vs. 13–16), perhaps because this gave more flexibility to accommodate upstream–downstream differences in survival. Differential mortality rates were very similar between those two types of models, whereas the regional models estimated a slightly larger average Ricker *a* parameter.

Correlation between variables

Using model 1, we examined estimates of μ (differential mortality) and δ (common year-effects) for correlations with other variables. There was a significant positive correlation ($r = 0.58$, $p < 0.01$) between μ and WTT (Fig. 4). The correlation was weaker but still significant even without the influential 1975 brood year ($r = 0.45$, $p < 0.05$). Some pairs of years with very similar WTT had very different values for μ (e.g., 1970 vs. 1972, 1974 vs. 1980, 1983 vs. 1989, and 1986 vs. 1990), suggesting that other factors besides WTT

Fig. 3. Comparison of median estimates of differential mortality (μ) using model 1 from Table 3 (thick, solid line), with estimates of μ from four mechanistic passage models (FLUSH T1, ●; FLUSH T2, ○; CRiSP T1, ■; CRiSP T2, □). The second *y* axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$).

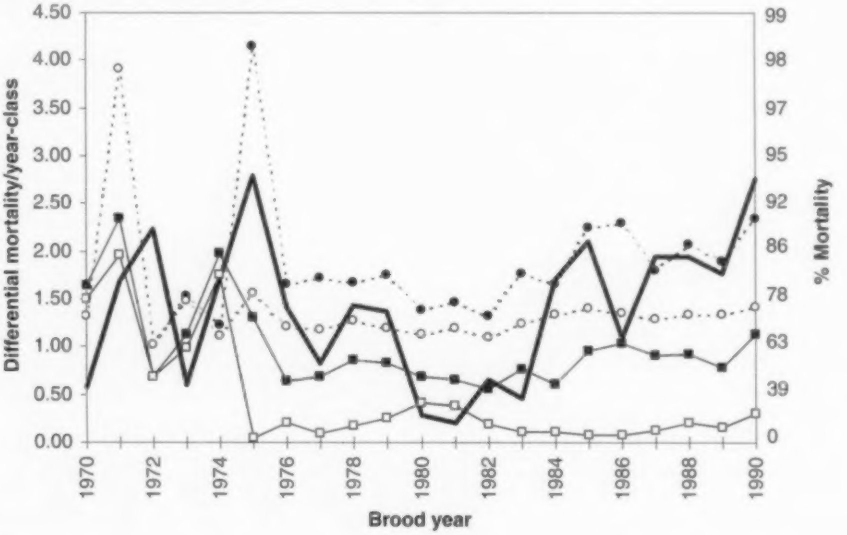
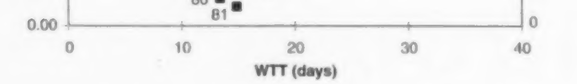


Fig. 4. Estimated differential mortality (μ) vs. water travel time (WTT). The regression line was fit through all of the data. The second *y* axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$). Solid diamonds represent the 1970s brood years; solid squares represent the 1980+ brood years.



influenced the value of μ in these years (Fig. 4). We separated the 1970–1979 and 1980–1990 periods to see if differences in power system management or other factors may have affected the correlation between WTT and μ. The 1970–1979 period showed a weaker correlation ($r = 0.58$, $p = 0.08$; without the 1975 datum $r = 0.06$, $p = 0.87$) than the 1980–1990 period ($r = 0.68$, $p = 0.02$). However, an analysis of covariance with WTT as the covariate showed no significant difference between the 1970s and 1980s ($p = 0.623$).

The year-effect (δ) reflects common factors affecting survival of all stocks. We therefore selected two general climate indicators (the North Pacific Index (NPI; Trenberth and Hurrell 1994) and an Upwelling Index) and WTT to see if they were correlated with δ. Correlation between δ and WTT was not significant ($r = -0.15$). NPI showed low correlations in all cases when matched to the first, second, and third ocean winter (i.e., r = 0.08, 0.26, and 0.33, respectively). The Upwelling Index was also not correlated with δ ($r = -0.09$). Interestingly, the standardized residuals of Bristol Bay sockeye survivals (Peterman et al. 1998) were negatively correlated with δ ($r = -0.51$). This is consistent with the hypothesis that ocean conditions experienced by salmon in the Northeast Pacific vary inversely with those experienced by salmon originating from Oregon and Washington (Mantua et al. 1997).

The correlation between MLE estimates of μ and δ ($r = -0.24$) in different years was not significant. Within-year estimates of the correlation of μ and δ were obtained by linear approximation around the MLE solution and are all moderately large numbers (around $r = 0.75$). The correlation structure presents a mixed picture: there is uncertainty about the relative influence of common year-effects and differential mortality within individual years, but the uncertainty is not so large as to support removal of year-effects from the model (compare models 29 and 30 with all others in Table 3). Between-year correlations are small so MLE estimates reasonably portray the larger pattern. The only obvious between-year pattern was that the brood year with the best year-effect (1983) also had a low differential mortality and the brood year with the worst year-effect (1990) also experienced high differential mortality.

Discussion

Stock–recruit models that best fit the spawner–recruit data included a common year-effect, excluded spawner measurement error, and included varying parameterizations of Ricker *a* and *m*. Our empirical estimates of differential mortality between upstream and downstream stocks with those models ranged from 42 to 85%. In general, MLE estimates of passage mortality from the empirical model 1 are intermediate between the CRiSP and FLUSH passage model estimates.

Mechanistic and empirical passage mortality estimates agreed better when mortality estimates from CRiSP and FLUSH were scaled. On the other hand, even the simple explanatory variable WTT could be used to model differential mortality with high performance (as in models 36 and 37).

The influence of in-river studies on the 1971 brood year (conducted on migrants in 1973, a low-flow year) has been profound in the debate over the effects of dams on mortality of smolts (e.g., Williams and Matthews 1995). Our results show that the 1973 study results are not consistent with observed returning recruits from the 1971 brood year. If the high mortality rate estimated by FLUSH for the 1971 brood year is correct (i.e., a differential mortality μ which is 3.4 above the μ given by model 1), then we must have had an exceptionally strong year-class for the 1971 brood year in terms of their natural survival to account for the observed spawner-to-recruit survival. In particular, the observed natural recruitment survival rate, $\ln(R/S)$ (i.e., excluding differential mortality) would have to be roughly 3.4 above the observed average R/S rate, which includes differential mortality. Adding 3.4 to the observed standardized $\ln(R/S)$ for brood year 1971 would place it about 1.0 above the maximum standardized survival for any other brood year for the up-river stocks. On the other hand, the high passage mortality for the 1975 brood year (1977 out-migration, another low-flow year) estimated by the passage models and by the empirical model 1 is generally consistent both with the observed $\ln(R/S)$ survival rate and with in-river studies conducted that year.

An alternative explanation for our results is that the decline in survival of up-river vs. down-river natural stocks was due to a marine mortality factor that differentially affected up-river and (or) down-river stocks in a large enough way to coincide with and account for the estimated differential mortality. However, models that included regional year-effects (models 22–28) generally performed worse than the empirical models that exclude this alternative hypothesis (e.g., model 1). In addition, despite intense scrutiny, within and outside of PATH, of this assumption using coded wire tag recovery data, no analyses to date clearly indicate systematic, regional differences between up-river and low-river stocks in ocean distribution or mortality (e.g., Marmorek et al. 1998; Schaller et al. 2000). Though it would be valuable to obtain better estimates of among-region differences in ocean distribution and survival of wild spring chinook, there are clearly not enough wild fish remaining to generate sufficient tag recoveries.

The models developed in this paper omit statistical covariance in the measurement errors. We did not attempt to model directly the process by which recruitment estimates were obtained by Beamesderfer et al. (1997), although such modeling is theoretically possible. The advantage of a more complete model for recruitment measurements is that we would then have the appropriate error structure for including the statistical covariance structure between recruitment measurement error and the several years of spawner-measurement error to which they contribute. Our opinion is that this covariance is likely low for two reasons. First, recruitment measurement errors originate from many important sources other than those induced by errors in escapement counts, including conversion rates applied at each dam to convert dam counts to total passage estimates, age distribution data, and correction for hatchery fish, and harvest removal. Second, chinook salmon return to the Columbia River to spawn (and hence become part of recruitment) over 4 or more years and thus the spawner-measurement error calculated in any given year would be applicable only to a portion of the recruitment from a given brood year. Other concerns are the presence of covariance in recruitment measurement errors among populations that share nearby sub-basins (such as the Snake River populations). We examined autocorrelation between recruitments in adjacent years and found that it had a negligible effect. Finally, another concern is that John Day Middle Fork stock, if excluded from the analysis, greatly reduces MLE estimates of up-river differential mortality and some sources of measurement error have been identified for this stock (Hinrichsen 2001); that concern has been debated within PATH without any resolution.

There is clearly uncertainty about the magnitude of differential mortality, year-effects, and Ricker a parameters. One way to address that uncertainty is to construct a single model that encompasses a range of alternative hypotheses about those parameter values and then conduct analyses that formally incorporate the uncertainty. Such a model is our model 1, which contains year-specific differential mortalities, common year-effects, and individual stock Ricker a parameters. It is in a virtual tie for best model according to the AIC criterion. Deriso (2001) describes the mechanics of generating prospective analyses for spring and summer chinook by application of Bayesian methods to model 1. The prospective modeling is part of a formal decision analysis of management actions designed to recover listed Snake River spring and summer chinook populations (Peters and Marmorek 2001).

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Application of decision analysis to evaluate recovery actions for threatened Snake River spring and summer chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: There is uncertainty about the importance of various factors in explaining declines of chinook salmon (*Oncorhynchus tshawytscha*) populations in the Snake River basin of Oregon and Idaho. This uncertainty has prevented implementation of long-term recovery actions for these stocks. We used simulation models and decision analysis to evaluate three management actions for seven index stocks of Snake River spring and summer chinook salmon: (*i*) continue current operation of the Columbia River hydropower system, (*ii*) maximize transportation of smolts, and (*iii*) natural river drawdown (breaching) of four Snake River dams. Decision analysis provided a useful approach for including multiple hypotheses about population responses to environmental and anthropogenic factors, systematically assessing the importance of alternative hypotheses, and identifying risk-averse recovery strategies that meet survival and recovery goals over a wide range of uncertainties. We found that the most influential uncertainties were related to hypothesized causes of estuary and ocean mortality. Current monitoring provides limited information on survival in this life stage; carefully designed management experiments are more likely to generate useful information. Given that these uncertainties exist, drawdown was the most risk-averse action, meeting long-term survival and recovery goals over a wider range of assumptions than the other actions.

Résumé : Il existe de l'incertitude au sujet de l'importance des divers facteurs explicatifs du déclin des populations de Saumons quinnat (*Oncorhynchus tshawytscha*) dans le bassin versant de la rivière Snake en Oregon et en Idaho. Cette incertitude a empêché la mise en oeuvre de stratégies de récupération à long terme de ces stocks. Des modèles de simulation et des analyses décisionnelles ont permis d'évaluer trois stratégies de gestion pour sept stocks indicatifs de saumons de printemps et d'été de la rivière Snake : (*i*) ou bien la poursuite de l'opération actuelle du système hydroélectrique du fleuve Columbia, (*ii*) ou alors la maximisation du transport des saumoneaux, (*iii*) ou enfin la baisse des eaux de la rivière à leur niveau naturel par ébrèchement de quatre barrages de la rivière Snake. L'analyse décisionnelle est une méthode utile pour incorporer des hypothèses multiples au sujet des réactions des populations aux facteurs environnementaux et anthropiques, pour évaluer systématiquement l'importance des hypothèses de rechange et pour identifier les stratégies de récupération qui évitent les risques tout en atteignant les objectifs de survie et de récupération sur une gamme étendue d'incertitudes. Les incertitudes les plus sérieuses concernent les causes présumées de la mortalité dans l'estuaire et l'océan. Le réseau de surveillance actuel ne fournit que peu de renseignements sur la survie à cette étape du cycle biologique; des expériences de gestion planifiées avec soin seraient plus susceptibles de générer des informations utiles. Étant donné l'existence de ces incertitudes, la baisse des niveaux des réservoirs est la stratégie qui pose le moins de risques et qui permet d'atteindre les objectifs de survie et de récupération à long terme sur une gamme plus étendue de pré-suppositions que les autres stratégies.

[Traduit par la Rédaction]

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) populations in the Snake River sub-basin of the Columbia River have declined over the last 100 years and are now listed as "threatened" under the United States Endangered Species Act (NMFS 1995). The decline in abundance has been particularly dramatic since the mid-1970s (Schaller et al. 1999), a period that saw the completion of the eight dams of the Federal Columbia River Power System (FCRPS), the start of a large-scale transportation program in which smolts are collected at upper dams and transported by truck or barge to below the lowermost dam, an increase in hatchery smolt production, the degrada-

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tion of freshwater spawning and rearing habitat in some natal streams, and an abrupt shift in climate conditions in the Northeast Pacific Ocean (Beamish et al. 1999).

Disagreements among scientists and policy makers about the relative contribution of these factors to declines in Snake River salmon populations led to the development of several alternative modeling frameworks for estimating the impacts of historical factors and predicting the effects of proposed management actions. Because each model differed in its underlying assumptions about which historical factors were most important, each suggested different optimal recovery strategies. After several years of debates and conflicting management advice, the models were subjected to technical review and comparison by a panel of experts, which recommended that modelers and policy makers work together to evaluate the underlying hypotheses that were ultimately responsible for differences among models (Barnthouse 1993). This focus on collaboratively evaluating model hypotheses was reiterated in a 1994 judicial ruling on a salmon-related lawsuit (IDFG v. NMFS, 850F, Supp. 886, D.Or. 1994) and in the National Marine Fisheries Service's 1995 Biological Opinion (a document that assesses the current status of stocks and prescribes specific recovery actions; NMFS 1995). These documents led to the formation of the Plan for Analyzing and Testing Hypotheses (PATH), a multiagency research program to identify and resolve biological uncertainties surrounding recovery of threatened Snake River chinook salmon and steelhead. PATH operated from September 1995 to May 2000. Strengths and weaknesses of the PATH process are described in Marmorek and Peters (2001).

PATH "retrospective" analyses of historical data attempted to identify major spatial and temporal patterns in abundance and productivity of Snake River salmon stocks over the last 40 years and to determine the relative influence of habitat, harvest, hatchery, hydrosystem, and climatic factors on these patterns (Marmorek et al. 1996*a*; Schaller et al. 1999; Botsford and Paulsen 2000). These analyses resolved some differences in underlying assumptions about what has affected stocks historically (Marmorek et al. 1996*b*; Barnthouse et al. 2000; Petrosky et al. 2001). However, significant uncertainties about the likely effects of future management actions on Snake River chinook stocks persist because of limitations in data on past and present conditions, different interpretations of existing data, and uncertainty about future conditions (e.g., trends in future climate conditions or the effects of new actions that have not been tried before). These uncertainties make it difficult to project the outcomes of alternative recovery policies and thus to identify the best policies to implement.

PATH used formal decision analysis (Clemen 1996; Peterman and Anderson 1999) to evaluate recovery strategies for Snake River ocean-type fall-run chinook salmon (Peters et al. 2001) and for seven index populations of stream-type spring- and summer-run chinook that spawn in tributaries to the Snake River upstream of Lower Granite Dam (this study). These seven index stocks were assumed to be representative of the entire Snake River spring and summer chinook Evolutionarily Significant Unit (a group of stocks that are considered to be genetically distinct under the Endangered Species Act). The objectives of the PATH decision analysis were to determine the relative influence of various sources of uncertainty on the outcomes of alternative actions and to assess the performance of alternative recovery actions across uncertainties.

Methods

Overview

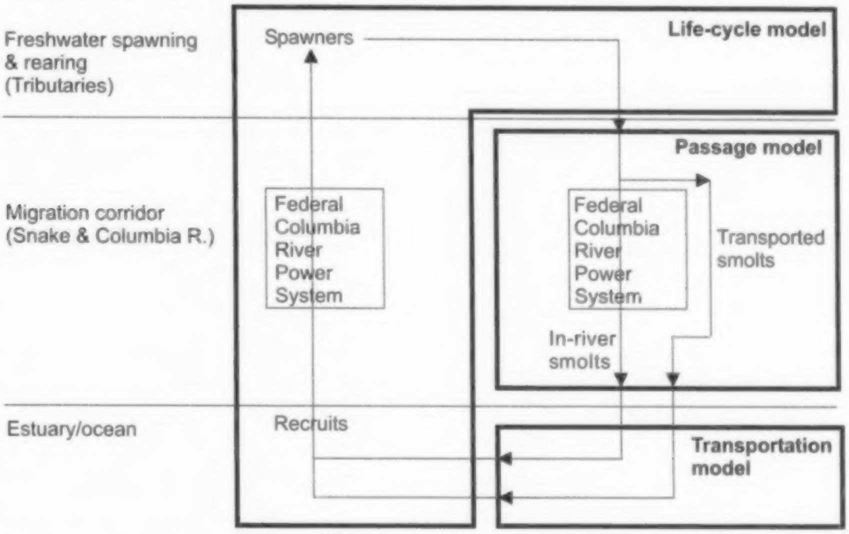
Decision analysis is a systematic approach to uncertainties in decision making using models to project outcomes of alternative actions. These outcomes (or performance measures) act as criteria for comparing and ranking the actions. Many possible outcomes are generated for each action, each resulting from a unique combination of alternative hypotheses about uncertain states of nature (for example, historical data may suggest that a range of spawner-to-recruit survival rates are possible). Such an approach has several benefits over approaches in which uncertainties are ignored or treated in an ad hoc manner. First, this approach can lead to more risk-averse management decisions in the long run because it allows decision makers to select "robust" actions that perform well under a broad range of assumptions. Implementing actions that are robust to uncertainties minimizes risks that the selected action will not have its intended effect, because such actions have a much higher chance of producing a favorable outcome even if the underlying hypotheses turn out to be wrong. Second, including uncertainties allows risk-averse actions to be identified and implemented before these uncertainties are fully resolved. This avoids the common situation in which uncertainties in the predicted effects of management actions discourage decision makers from changing management policies from the status quo (Peterman and Anderson 1999). Avoiding such inaction is particularly important for endangered species, where recovery actions generally need to be taken long before uncertainties can be resolved to the satisfaction of decision makers. Third, explicitly incorporating alternative hypotheses about key uncertainties allows scientists and agencies with alternative interpretations of existing data to participate in collaborative analytical processes.

There were seven components of the PATH decision analysis: alternative actions, performance measures, models, uncertainties, probabilities on alternative hypotheses, an overall decision analysis framework, and sensitivity analyses. Each component is described below.

Alternative actions to be evaluated

The PATH decision analysis focused primarily on three recovery actions related to the configuration and operation of eight Federally owned and operated dams on the Columbia and lower Snake rivers. Action A1 represented current operation of these dams as prescribed by the 1995 Biological Opinion (NMFS 1995) and was therefore most similar to a status quo action. This action assumed that all of the measures called for in the 1995 Biological Opinion are implemented in full in every year. With action A2, the hydropower system is operated to collect as many fish as possible at the uppermost dams for transport by barge past the hydropower system and release below Bonneville Dam (the last dam encountered by juvenile salmon as they migrate to the ocean). Action A3 was drawdown to natural river levels of the four dams on the lower Snake River (Lower Granite, Little Goose, Lower Monumental, and Ice Harbor). Under this action, a 222-km unimpounded reach would be created by removing earthen berms adjacent to these dam structures. Hydroelectricity generation and navigation at these projects would be eliminated. We also evaluated three variations on actions A1, A2, and A3 but do not report their results here because

Fig. 1. Schematic diagram of the life cycle of Snake River spring and summer chinook salmon. The passage models estimated survival of smolts in the Columbia and Snake rivers as they pass through (in-river smolts) or around (transported smolts) the eight dams of the Federal Columbia River Power System (FCRPS). Transportation models estimated the relative estuary and ocean survival rate of transported and in-river smolts. Life-cycle models estimated survival rates over the rest of the life cycle (spawners in natal streams to smolts at the top of the hydropower system and from smolts at the bottom of the hydropower system through estuary and ocean residence and upstream migration back to spawners in their natal streams).



they produced similar outcomes to the three primary actions (Marmorek et al. 1998*c*).

Performance measures used to evaluate the actions

Performance measures provided a quantitative indicator of how well alternative management actions performed, both relative to other actions and with respect to absolute goals for survival and recovery of listed stocks. PATH used the "jeopardy standards" generally accepted by NMFS for Snake River chinook salmon (NMFS 1995). There were two types of standards: survival and recovery. The survival standard was based on the probability (over 3000 Monte Carlo simulations) that the projected number of spawners for individual stocks would exceed survival escapement thresholds of either 150 or 300 spawners. These probabilities were calculated over 24 and 100 simulation years to reflect short- and long-term effects. The recovery standard was based on the probability that the projected spawning abundance of a stock will be above a specified recovery escapement threshold (thresholds for the seven index stocks ranged from 350 to 1150 spawners). This probability was calculated over the last 8 years of a 48-year simulation. As an absolute standard for evaluating actions, PATH specified that most stocks should have survival probabilities of at least 0.7 (i.e., stocks exceed their survival escapement threshold in at least 70% of the simulated years) and recovery probabilities of at least 0.5. See the Appendix for details on how these probabilities were calculated.

Models to project outcomes of actions

The PATH modeling framework for the decision analysis used passage, transportation, and life-cycle models to represent the entire life cycle of spring and summer chinook salmon (Fig. 1). The modeling analysis proceeded in two linked steps: retrospective and prospective (Fig. 2). Retrospective modeling captured our understanding of the past by generating distributions of historical estimates of key model parameters. Prospective modeling used these distributions of historical estimates as the basis for assessing the range of possible future outcomes of management actions.

Retrospective passage and transportation modeling

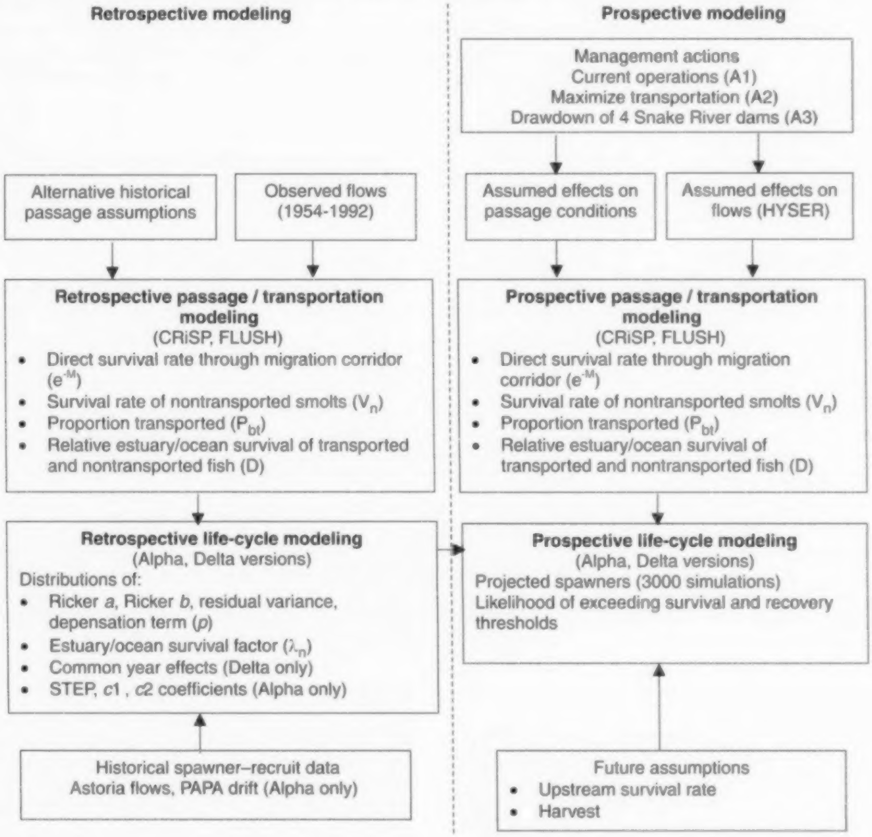
Retrospective passage and transportation modeling generated historical estimates (for brood years 1952–1990) of four parameters related to the passage of smolts through the migration corridor: (*i*) direct passage survival rate (e^{-M}, where M is the instantaneous mortality rate through the migration corridor), the weighted average survival rate of transported smolts and in-river smolts (smolts that are not collected for transportation but are allowed to migrate through the dams and reservoirs of the FCRPS), measured from the top of the reservoir of the first dam encountered (Lower Granite) to below the last dam (Bonneville); (*ii*) survival rate of in-river smolts from the head of Lower Granite reservoir to below Bonneville Dam (V_n); (*iii*) proportion of all smolts arriving below Bonneville Dam that were transported (P_{bt}); and (*iv*) estuary and ocean survival rate of transported fish relative to that of in-river fish (this ratio is called D; see Appendix for details on how D was estimated). $D < 1$ suggests that transported fish have lower estuary and ocean survival rates than in-river fish, whereas $D > 1$ suggests that transported fish survive better than in-river fish through this life stage.

Estimates of passage and transportation parameters depended on assumptions about historical passage conditions (such as the mortality of fish at specific dams in past years), the success of past transportation experiments, and observed flows over the historical period. The terms e^{-M}, P_{bt}, and D were combined to produce an estimate of system survival (ω), the weighted average survival rate of all smolts (transported and in-river) through the hydropower system with the survival rate of transported fish discounted by their hypothesized survival disadvantage in the estuary and ocean (see Appendix for details).

Retrospective life-cycle modeling

Estimates of the four passage and transportation parameters were

Fig. 2. Modeling approach used in the decision analysis. Retrospective modeling (left side of diagram) described and explained historical patterns in spawner-to-recruit survival rates. Results were expressed as distributions of parameters, which were passed to the prospective models. In the prospective phase (right side of diagram), retrospective results were used to forecast the response of stocks to alternative management actions under a range of assumptions and hypotheses. See text for definition of terms.


Retrospective modeling
Prospective modeling
Management actions
Current operations (A1)
Maximize transportation (A2)
Drawdown of 4 Snake River dams (A3)
Alternative historical passage assumptions
Observed flows (1954-1992)
Assumed effects on passage conditions
Assumed effects on flows (HYSER)
Retrospective passage / transportation modeling
(CRiSP, FLUSH)
• Direct survival rate through migration corridor (e^{-M})
• Survival rate of nontransported smolts (V_n)
• Proportion transported (P_{bt})
• Relative estuary/ocean survival of transported and nontransported fish (D)
Prospective passage / transportation modeling
(CRiSP, FLUSH)
• Direct survival rate through migration corridor (e^{-M})
• Survival rate of nontransported smolts (V_n)
• Proportion transported (P_{bt})
• Relative estuary/ocean survival of transported and nontransported fish (D)
Retrospective life-cycle modeling
(Alpha, Delta versions)
Distributions of:
• Ricker a, Ricker b, residual variance, depensation term (p)
• Estuary/ocean survival factor (λ_n)
• Common year effects (Delta only)
• STEP, c1 , c2 coefficients (Alpha only)
Prospective life-cycle modeling
(Alpha, Delta versions)
Projected spawners (3000 simulations)
Likelihood of exceeding survival and recovery thresholds
Historical spawner–recruit data
Astoria flows, PAPA drift (Alpha only)
Future assumptions
• Upstream survival rate
• Harvest

passed to the life-cycle model, along with historical spawner–recruit estimates (Beamesderfer et al. 1997) and environmental data (e.g., climate indices) from brood years 1952–1990. The life-cycle model was a generalized version of a Ricker stock–recruit model. We developed two versions of this model: an "Alpha" version (Anderson and Hinrichsen 1997) and a "Delta" version (Deriso et al. 2001). The two versions embodied different assumptions about the existence of common mortality effects that affect both Snake River and lower Columbia River stream-type chinook stocks and used different methods for calculating estuary and ocean survival factors for in-river fish (λ_n). The Delta model assumed that Snake and lower Columbia stocks experience common mortality effects and calculated estuary and ocean survival factors indirectly from estimated overall (spawner to recruit) survival rates. The Alpha model allowed for different responses to ocean climate and other factors in different regions within the Columbia River basin and calculated estuary and ocean survival rates directly from various climatic factors such as Columbia River flows at its mouth. Both versions estimated posterior probabilities of model parameters. The two versions are described further in the Appendix.

Prospective passage and transportation modeling

Prospective passage and transportation modeling projected future values for the four passage-related parameters (M, V_n, P_{bt}, D) based on assumptions about how the alternative management actions would affect flows and conditions that determine passage survival. Such conditions included the efficiency of bypass systems that route fish around turbines, the amount of spill at individual projects, and dam configurations and operations in future years. A hydro-regulation model (HYSER) developed by the U.S. Army Corps of Engineers translated each management action into mean monthly flows at various locations in the Snake and Columbia rivers, given the natural runoff conditions that were observed from 1977 to 1992. These years were chosen because they were most representative of current operations and conditions. The HYSER model generated 16 sets of mean monthly flows, one for each of these years. The passage models projected a set of the four passage-related parameters for each action, for each of the assumptions about the effect of that action on passage conditions, and for each year of monthly mean flows generated by the HYSER model for that action. For example, a parameter set projected with 1982 mean monthly flows represented the passage- and transportation-related survival rates expected to prevail if a given action were implemented, if that action had the assumed affect on passage conditions and flows, and if 1982 runoff conditions occurred.

Prospective life-cycle modeling

The life-cycle model combined posterior probability distributions of life-cycle parameters from the retrospective modeling, sets of downstream passage parameters from the prospective passage modeling, and assumptions about other future influences on survival (i.e., adult survival during upstream migration, harvest rates, habitat changes) into projections of spawning abundance for each of the seven Snake River index stocks over a 100-year simulation period beginning in brood year 1996 (Deriso 2001). In each of the 3000 Monte Carlo simulations, a set of life-cycle model parameters (i.e., Ricker *a*, Ricker *b*, *p*, residual variance) was selected from the distributions generated from the retrospective analyses. In each year of a simulation, the model also selected annual estuary and ocean survival factors (λ_n) and climate-related survival factors according to alternative hypotheses about how these factors would change in response to management actions (see next section), and a particular "flow year" from 1977 to 1992 according to how frequently the natural runoff in each of those years occurred in the 1929–1992 historical record. The selected flow year determined which of the 16 sets of prospective passage-related parameters was used for that year of the simulation.

Uncertainties that determine the range of possible outcomes for each action

Uncertainty in Ricker *a*, Ricker *b*, and other life-cycle parameters was incorporated into the forward projections through Monte Carlo analyses that sampled from the joint posterior distribution of these parameters. PATH scientists also included 11 additional discrete uncertainties in the decision analysis (Table 1). These uncertainties were selected either because they were major assumptions that PATH retrospective analyses had not sufficiently resolved because of data limitations or differences in interpretation of data or because they were related to future conditions and thus not addressed by the retrospective analyses. For each uncertainty, we formulated two or three alternative hypotheses about how the uncertainty was expected to affect the outcomes of actions. Alternative hypotheses took the form of different parameter values in the passage–transportation or life-cycle models, or different approaches to selecting from historical distributions of parameters in forward projections. Further details and rationale for all hypotheses can be found in Marmorek et al. (1998*a*, 1998*b*).

Juvenile passage survival rate

Values of e^{-M}, V_n, and P_{bt} were computed by two passage models: CRiSP (Columbia River Salmon Passage model, developed by researchers at the University of Washington for the Bonneville Power Administration; Anderson et al. 1996), and spring FLUSH (Fish Leaving Under Several Hypotheses, developed by State and Tribal researchers; Wilson 1994).

Fish guidance efficiency

Fish Guidance Efficiency (FGE) measures the ability of submerged screens to divert fish away from turbines into bypass systems with lower mortality rates than turbines. Extended-length screens have been installed at some dams in recent years, but their relative effectiveness in diverting fish to the bypass systems was uncertain.

Turbine and bypass mortality

Current estimates of turbine and bypass mortality rates for spring and summer chinook smolts are generally accepted, but there was uncertainty about the importance of direct physical injury (descaling) in causing mortality at some dams before 1980.

Predator-removal effectiveness

Since 1990, bounties have been offered for catching northern pikeminnow (*Ptychocheilus oregonensis*), a predator of migrating salmon smolts in reservoirs along the Columbia and Snake rivers. Uncertainty about the degree of compensatory responses of predator populations to the removal program led to disagreement about the effect of the program on survival rates of salmon smolts.

Transportation assumptions

Transportation assumptions were important because under current operating regimes, over 90% of smolts below Bonneville Dam arrive there by barge. Hypotheses about the effectiveness of transporting fish past the hydrosystem focused on the survival rate of transported fish, once they are released from the barge, relative to in-river fish (represented by *D* values). Each passage model developed its own set of historical and future *D* values (see details in Appendix) based on interpretations of results of past transportation and survival studies (Fig. 3). Future *D* values depended on assumptions about the applicability of historical transportation conditions to future simulations.

Regional mortality effects

There is uncertainty about the existence of common mortality effects that influence both Snake River and lower Columbia River stream-type chinook stocks (Schaller et al. 1999, 2000; Zabel and Williams 2000). The two versions of the life-cycle model (Alpha and Delta) embodied different assumptions about these effects and used different methods for calculating estuary and ocean survival factors for in-river fish (see Appendix).

Future climate

Short- to medium-term variation in future climate and its effects on survival rates was modeled by drawing from the historical distributions of climate factors estimated from retrospective modeling. Two sampling approaches were used to reflect possible patterns in future climate conditions. Longer-term climate cycles were considered in the Regime Shift hypothesis (described below).

Estuary and ocean survival factor for in-river fish (λ_n)

Historical distributions of estuary and ocean survival factors (λ_n) were estimated by the life-cycle model through retrospective modeling. These estimates were based on observed patterns in survival to adulthood of the seven Snake River index stocks (which migrate past 8 mainstem projects) and six conspecific downstream "control" stocks (which migrate through 1, 2, or 3 projects) (Deriso et al. 2001; Schaller et al. 1999). Between the pre-1970 and post-1974 periods, the survival rate of Snake River stocks declined significantly more than the downstream stocks. This suggested that some fundamental change in survival conditions occurred in the mid-1970s and that the effect of this change on Snake River fish was systematically different from the effect on downstream stocks.

The decline in survival rates in the mid-1970s coincided with several major changes in environmental and anthropomorphic influences on salmon, including the completion of the final two Federal dams on the lower Snake River, a substantial increase in hatchery production, and a shift in climate conditions in the Northeast Pacific Ocean. We developed three hypotheses (Hydro, Stock Viability, and Regime Shift) to account for possible effects of these changes on estuary and ocean survival rates of Snake River fish. These hypotheses provided alternative explanations for historical patterns in survival and had implications for how λ_n was expected to change in response to future management actions. For example, the Hydro explanation for historical survival patterns implied that the survival factor λ_n would increase significantly when dams were breached under the drawdown action (A3). More details on these hypotheses and how they were implemented in the life-cycle model are provided in the Appendix.

Duration of pre-removal period

The pre-removal period represented the length of time between a decision to proceed with drawdown and the start of construction work to breach dams. Assumptions about the duration of this period depended on the expected length of the Congressional approval and appropriations process and the possibility of litigation.

Table 1. Uncertainties and alternative hypotheses incorporated into the PATH decision analysis.

Uncertainty	Alternative hypotheses
Total passage mortality (M), in-river survival rate (V_n), and proportion transported (P_{bt})	CRiSP passage model: mechanistic model with a daily time step. CRiSP survival rates through the FCRPS generally higher than FLUSH values. Spring FLUSH passage model: more aggregated, empirical approach with a seasonal time step.
Fish guidance efficiency (FGE)	Extended-length screens increase FGE. Extended-length screens do not increase FGE.
Turbine and bypass mortality before 1980	Higher turbine and bypass mortality: assumed turbine and bypass mortality entirely due to descaling. Lower turbine and bypass mortality: assumed turbine and bypass mortality partially due to descaling.
Predator-removal effectiveness	0% reduction in reservoir mortality: assumed high compensatory response by predators. 25% reduction in reservoir mortality: assumed low compensatory response by predators.
Transportation assumptions (D)	Transportation assumptions associated with FLUSH passage model: low survival rates of transported fish relative to in-river fish (median post-1980 $D = 0.34$) because of increased stress, deterioration of homing ability, and other mechanisms (Budy et al. 2002). Transportation assumptions associated with CRiSP passage model: high survival rates of transported fish relative to in-river fish (median post-1980 $D = 0.63$).
Regional mortality effects	Delta model: upstream and downstream stocks experience common climate effects Alpha model: upstream and downstream stocks respond independently to climate effects
Future climate Delta version: represented by δ (common year-effect) Alpha version: represented by E (latitude of a drifting object 3 months after release from ocean station PAPA in the Northeast Pacific Ocean)	Future simulations sample δ (Delta version) or E (Alpha version) either (*a*) from good or bad historical periods according to an 18.5-year cycle in ocean conditions (Beamish et al. 1999) or (*b*) with first-order autocorrelation from historical distributions for 1950–1995 (a period with both good and bad climatic conditions).
Estuary and ocean survival factor for in-river Snake River fish. Delta version: represented by λ_n Alpha version: represented by STEP	Hydro: estuary and ocean survival factor related to delayed effects of passage through the eight dams of the Federal Columbia River Power System (Budy et al. 2002). Stock viability: current (1977–1992) estuary and ocean survival rates will continue indefinitely in the future, even if hydrosystem direct mortality declines or climate improves. Regime shift: estuary and ocean survival factor follows long-term (60-year) cycle in ocean climate that affected Snake River fish more severely than downstream stocks after the mid-1970s.
Duration of pre-removal period under drawdown	3 years 8 years
Juvenile survival rate after drawdown	Survival rate through drawndown Snake River reach = 0.96 (average Snake River survival rate estimated before three of four Snake River dams were built; Raymond 1979); survival rates through the entire Snake and Columbia rivers (with only four dams in place) = 0.64 (CRiSP) and 0.56 (FLUSH). Assumed drawdown eliminates direct dam mortality, reduces reservoir habitats favored by predators, and restores more natural flows. Survival rate through drawndown Snake River reach = 0.85 (current estimate of average survival rates through the free-flowing stretch of the Snake River above Lower Granite Dam); survival rates through the entire Snake and Columbia rivers (with only four dams in place) = 0.55 (CRiSP) and 0.50 (FLUSH). Assumed drawdown only eliminates direct dam mortality; changes in predators and flow regimes since placement of dams are permanent and not affected by drawdown.
Duration of transition period after drawdown	2 years: processes equilibrating in a relatively short period of time (e.g., sediment removal, redistribution of predators) are more important for juvenile survival rates. 10 years: processes taking longer to equilibrate (stabilization and recolonization of banks, population responses by predators) are more important.

Note: Alternative hypotheses took the form of different parameter values in the passage–transportation or the life-cycle models or different approaches to selecting from historical distributions of parameters in forward projections. CRiSP, Columbia River Salmon Passage; FCRPS, Federal Columbia River Power System; FLUSH, Fish Leaving Under Several Hypotheses.

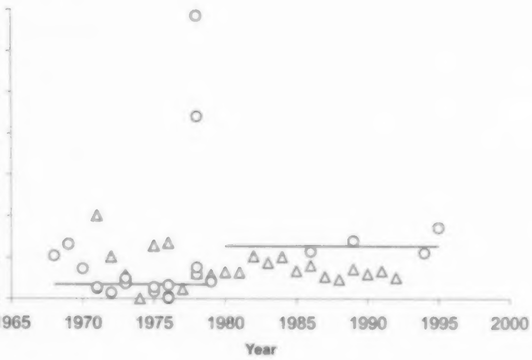


Fig. 3. Retrospective D values estimated by the FLUSH (Fish Leaving Under Several Hypotheses, triangles) and CRiSP (Columbia River Salmon Passage, circles) transportation models. See Appendix for details of each model's method. CRiSP values used in the retrospective analysis for periods 1968 to 1979 and 1980 to 1992 (horizontal lines) were the median of CRiSP estimates during those periods (0.174 and 0.633, respectively).

Juvenile survival rate after drawdown

Once implemented, drawdown of dams was assumed to eventually improve juvenile survival rates by eliminating direct dam mortality, reducing predation mortality in reservoirs, and restoring more natural flows. Because the extent to which all of these benefits would be realized was uncertain, we developed two hypotheses about post-drawdown juvenile survival rates. Under these hypotheses, post-drawdown survival rates of juveniles through the entire Snake and Columbia rivers (with four dams in place) ranged from 0.50 to 0.64 depending on the hypothesis and passage model. In comparison, average in-river survival rates through the existing hydropower system (i.e., all eight dams in place) were 0.24 (with FLUSH) and 0.39 (with CRiSP).

Duration of transition period

The transition period was the length of time between completion of dam removal and establishment of a dynamic equilibrium in the drawndown section of the river. Although there was general agreement that initially dam drawdown would likely disrupt physical and biological processes in the river, there were no case studies to suggest how long it would take for these processes to equilibrate.

Probabilities on alternative hypotheses

Decision analysis requires probabilities on the alternative hypotheses that reflect their relative likelihood, or strength of empirical support. Initially, for the purposes of conducting sensitivity analyses and seeing which of the uncertainties had the most influence on the outcomes of actions, we assumed that all hypotheses were weighted equally. However, we recognized that some hypotheses had more empirical support than others. Therefore, after completing preliminary sensitivity analyses and identifying key uncertainties (i.e., those most affecting modeled outcomes), we initiated a Weight of Evidence process to systematically compile the evidence and assess the relative merits of alternative hypotheses (appendix 4 in Marmorek and Peters 2001). Weights on alternative hypotheses were then elicited from four scientists on the independent PATH Scientific Review Panel based on the evidence available as of August 1998 (Table 2). Since 1998, new data and analyses have become available that may affect the weights assigned to alternative hypotheses. Therefore, it may be worthwhile to systematically compile and evaluate this new information and elicit a new set of weights from independent scientists. The PATH Weight of Evidence process provides an example of a collaborative approach to assessing evidence.

Decision analysis framework

We used a "decision tree" as a graphical tool for integrating actions, performance measures, models, and uncertainties into a logical evaluation framework (a highly simplified form of the PATH decision tree is shown in Fig. 4). The 11 uncertainties and their alternative hypotheses resulted in 240 possible outcomes for actions A1 (current operations) and A2 (maximize transportation) and 1920 possible outcomes for action A3 (natural river drawdown of four Snake River dams). Each outcome was based on 3000, 100-year prospective Monte Carlo simulations, each selecting a different set of life-cycle model parameters (Ricker a, Ricker b, p, residual variance) from their joint probability distribution.

These sets of outcomes provided the basis for identifying key uncertainties and evaluating the performance of actions across uncertainties. To identify which uncertainties had the most influence on outcomes, we applied a Categorical Regression Tree (CART; Breiman et al. 1984; Watters and Deriso 2000) analysis to the complete set of outcomes for all actions. The CART analysis used a sum-of-squares criterion to find the factors that explain most of the overall variation in the set of outcomes ($R^2 \geq 0.95$). We used the frequency distribution of outcomes (summarized with box-and-whisker plots) as an indication of how well each action performed over the full range of uncertainties.

Sensitivity analyses

Although PATH's primary focus was on evaluating hydrosystem actions, the PATH modeling structure was sufficiently flexible to allow consideration of non-hydro mortality factors such as freshwater spawning and rearing habitat, mainstem and tributary harvest, and avian predation in the estuary. Decision analysis provided a convenient framework for exploring the effects of hypothetical actions in these non-hydro areas. We do not report the results of these analyses here because we found that the effects of these non-hydro actions were generally not as significant as effects of hydrosystem actions, unless dramatic changes were made (e.g., permanent elimination of all mainstem commercial and sport fisheries and conservation-level tribal ceremonial fisheries) (Marmorek et al. 1998*c*).

Results

Relative effects of uncertainties

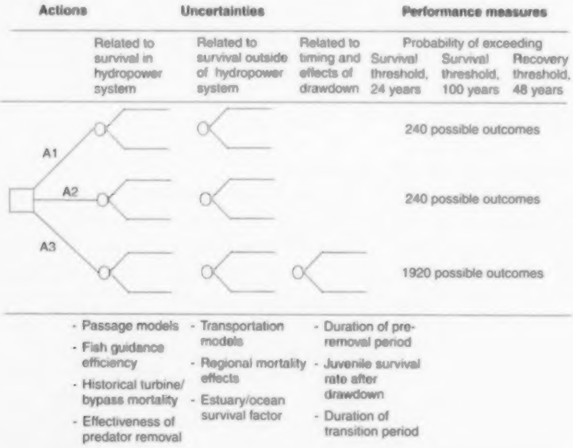
Assumptions associated with the alternative actions were most important in determining the 100-year probability of exceeding the survival threshold and the 48-year probability of exceeding the recovery threshold (Fig. 5; the CART tree for the probability of exceeding the survival escapement threshold over 100 years is similar to the CART tree for the 48-year recovery metric). That is, the effects of differences in the operation and configuration of the hydropower system associated with the different actions (e.g., differences between current and post-drawdown in-river survival rates) were more important in determining stock recovery than the effects of the 11 uncertainties described in Table 1. Of the uncertainties, regional mortality effects (Alpha vs. Delta models) and the cause of estuary and ocean mortality (hydro vs. stock viability vs. regime shift) were most important for

Table 2. Weights placed on alternative hypotheses by the four members of the PATH Scientific Review Panel (SRP).

Key uncertainty	Alternative hypothesis	Relative weights			
		1	2	3	4
Passage–transportation models	FLUSH	0.7	0.75	0.9	0.65
	CRiSP	0.3	0.25	0.1	0.35
Estuary and ocean survival factor for in-river fish	Stock viability	0.3	0.25	0.495	0.4
	Hydro	0.6	0.60	0.495	0.4
	Regime shift	0.1	0.15	0.010	0.2
Regional mortality effects	Alpha life-cycle model	0.0	0.7	0.1	0.1
	Delta life-cycle model	1.0	0.3	1.0	0.9
Length of transition period	2 years	0.6	0.33	0.2	0.5
	10 years	0.4	0.67	0.8	0.5
Turbine and bypass mortality before 1980	Upper bound	0.6	0.4	0.4	0.5
	Lower bound	0.4	0.6	0.6	0.5
Predator-removal effectiveness	0% reduction in reservoir mortality	0.7	1.0	0.8	0.9
	25% reduction in reservoir mortality	0.3	0.0	0.2	0.1
Juvenile survival rate after drawdown	0.85	0.6	0.8	0.8	0.25
	0.96	0.4	0.2	0.2	0.75

Note: Weights reflect each SRP member's judgement on the relative likelihood of each hypothesis, based on their assessment of the evidence provided by PATH (Marmorek et al. 1998*b*). Alternative hypotheses are described in the text and in Table 1. FLUSH, Fish Leaving Under Several Hypotheses; CRiSP, Columbia River Salmon Passage.

Fig. 4. Decision tree summarizing the decision analysis of recovery actions for Snake River spring and summer chinook salmon. The three actions to evaluate emanate from the "decision node" (square box) on the left. A1 is current operations, A2 is maximize transportation, and A3 is natural river drawdown of four lower Snake River dams. The circles represent "chance nodes", with branches indicating alternative hypotheses about the possible effects of each uncertainty on the outcomes. Each pathway along the branches represented a particular combination of alternative hypotheses, each of which produced a unique set of performance measures (probability of exceeding survival escapement thresholds over 24 and 100 years and probability of exceeding recovery escapement thresholds over 48 years) as shown on the right side of the tree. The tree is highly simplified for illustrative purposes (i.e., not all possible pathways are shown).


Actions
Uncertainties
Performance measures
Related to survival in hydropower system
Related to survival outside of hydropower system
Related to timing and effects of drawdown
Probability of exceeding
Survival threshold, 24 years
Survival threshold, 100 years
Recovery threshold, 48 years
A1
A2
A3
240 possible outcomes
240 possible outcomes
1920 possible outcomes
- Passage models
- Fish guidance efficiency
- Historical turbine/bypass mortality
- Effectiveness of predator removal
- Transportation models
- Regional mortality effects
- Estuary/ocean survival factor
- Duration of pre-removal period
- Juvenile survival rate after drawdown
- Duration of transition period

the drawdown action A3 (right side of Fig. 5), and passage–transportation models (CRiSP vs. FLUSH) were most important for actions A1 (current operations) and A2 (maximize transportation) (left side of Fig. 5). Further sensitivity analyses of the two passage and transportation models showed that the key difference between them was in their estimates of *D* (particularly the retrospective estimates), rather than in their estimates of direct hydropower survival (M, V_n, or P_{bt}; Marmorek et al. 1998*b*).

Uncertainties related to the cause of mortality of in-river fish in the estuary and ocean and the effectiveness of transportation (*D*) were the most important factors in determining the 24-year probability of exceeding the survival threshold (Fig. 6) and generally had more influence on outcomes than the actions. The projected escapement of stocks in the short term depended more on assumptions about these components of stock dynamics than on what actions were taken because drawdown actions were assumed to generate their maximum survival benefits only after 7–20 years (i.e., after the pre-removal, construction, and transition periods).

Performance of actions across uncertainties

Actions A1 (current operations) and A2 (maximize transportation) produced similar distributions of probabilities of exceeding survival and recovery thresholds (Fig. 7). A1 outcomes were actually slightly higher than A2 because spill (which generally produces a higher survival rate for smolts than going through turbines) was eliminated under A2 at several dams, whereas the proportion of fish transported in A2 was only slightly higher than that in A1. Means and medians of the distributions for these two actions were slightly below the standards for recovery (0.5) over 48 years and survival (0.7) over 24 years but slightly over the survival standard over 100 years. Around 65% of the 240 possible outcomes for both actions were below the survival standard of 0.7 over 24 years, 30% of the outcomes were below the 0.7 survival standard over 100 years, and 55% were below the 0.5 recovery standard over 48 years.

Outcomes for action A3 (natural river drawdown of four lower Snake River dams) were generally higher than for the other actions and had narrower distributions. Mean and median probabilities of exceeding the survival thresholds barely exceeded the 0.7 standard over 24 years but were well over the survival standard over 100 years and the 0.5 recovery standard over 48 years. Forty-five percent of the 1920 possible outcomes for A3 were below the 0.7 survival standard over 24 years, but virtually none of the outcomes was below the longer-term survival and the recovery standard.

Discussion

The PATH decision analysis helped to focus scientific debate on the key underlying hypotheses that account for differences in the results and implied recovery strategies of alternative modeling systems. Specifically, we found that the uncertainties that had the largest influence on the relative outcomes of actions were those related to the patterns and causes of mortality of Snake River chinook in the estuary and ocean life stage (e.g., relative estuary and ocean survival rates of transported and in-river fish *(D)*, factors affecting estuary and ocean survival factors of in-river fish (λ_n), and regional patterns in estuary and ocean mortality effects). These uncertainties exist because rearing, migration, and estuary and ocean conditions changed at the same time that survival rates of Snake River fish began to decline dramatically.

Uncertainty about the cause of mortality in the estuary and ocean is unlikely to be resolved in the near future because existing monitoring programs provide equivocal information on survival rates through this life stage. For example, adult returns have been too low to provide reliable estuary and ocean survival estimates using PIT (passive induced transponder) tags. Similarly, recoveries of coded-wire tags have been too few to provide unambiguous information on ocean distributions of Snake River and downstream stream-type chinook stocks (Paulsen and Fisher 1997; Marmorek et al. 1998*b*). Such information is necessary to determine the importance of ocean conditions in observed differences in historical patterns of ocean survival rates between different stock groups (Schaller et al. 1999). Transportation studies using PIT-tagged groups of transported and in-river groups of fish are designed to yield specific information on relative smolt-to-adult survival rates of these different groups and have been conducted since the late 1960s. However, the time series of data from these studies is confounded by changes in study methods over time (e.g., freeze branding vs. PIT tagging, trucking vs. barging). Current transportation studies are much improved over previous methods but still require various assumptions and produce distributions of *D* estimates under current, but not historical, conditions (NMFS 1999; Bouwes et al. 1999). Sensitivity analyses showed that historical *D* estimates were an important determinant of model outcomes.

Although new data and analyses are not likely to resolve key uncertainties, they may lead to the formation of new alternative hypotheses and weighting schemes. The PATH decision analysis provides a convenient framework for exploring the implications of additional hypotheses and alternative weighting schemes. However, these new hypotheses and weights should be developed and evaluated based on all available empirical evidence, not on their effects on projected outcomes of alternative recovery strategies.

Constraints on current monitoring programs, coupled with the confounding associated with implementing many different management actions at the same time, suggest that the best and perhaps only way to resolve key uncertainties is to implement large-scale management experiments and concurrent monitoring of survival rates over both the whole life cycle and specific life stages. PATH has completed a preliminary evaluation of some potential management experiments, the results of which indicate that well-designed experiments can reduce confounding and provide information on the factors that affect both overall and life stage specific survival rates (Peters et al. 2000; C. Paulsen, 16016 SW Boones Ferry Road, Lake Oswego, OR 97035, unpublished data). Although it is often difficult to implement experimental management with endangered species because of regulatory and logistical restrictions, the need for experimental management can be greater in these situations because the high political and social costs of decisions regarding endangered species generally cause decision makers to demand higher levels of certainty than are achievable with standard monitoring approaches.

Given the existence of several key uncertainties unlikely to be fully resolved in the short term, a biologically risk-averse approach to choosing a recovery strategy is to implement a "robust" action that achieves survival and recovery goals over a broad range of assumptions. Such an approach avoids relying on an unlikely or infrequent set of conditions to recover the stocks and thus minimizes the likelihood of "surprise" outcomes over the long term. Moreover, explicitly including uncertainties in the analysis of alternative actions allows the identification of a robust course of action now, without having to wait for these uncertainties to be resolved. Our results suggest that natural river drawdown of the four lower Snake River dams was the most robust action, meeting the 100-year survival and 48-year recovery goals over virtually all of the hypotheses and assumptions included in the decision analysis. This result suggests that we can be relatively confident that the drawdown action will meet long-term survival and recovery goals, even if we are not sure which of our hypotheses is correct. Neither drawdown nor the transportation action was able to achieve short-term survival targets with any certainty because of the low numbers of spawners in recent years.

As in any modeling exercise, we have included various assumptions, and excluded others, to represent a complex world in a simplified quantitative model. Although we have captured what we think are the most important components for evaluating hydrosystem actions, we acknowledge that the absolute predictive power of our models is probably low. Subsequent to the completion of the PATH modeling exercise, spawner estimates were generated for brood years 1996–1999. Predicted spawner numbers from our models for that period were generally higher than the actual estimates, suggesting that our modeled escapements were probably optimistic. The primary reason for this was that our simulations assumed that future climate conditions would resemble those from brood years 1952–1991 and conditions that determine passage-related mortality would resemble those from brood years 1975–1990. Both periods included good and bad conditions for salmon production, but the overall average conditions over the entire time periods were consider-

Fig. 5. Categorical Analytical Regression Tree (CART) diagram showing the relative influence of actions and uncertainties on the probability of exceeding the recovery escapement threshold over 48 years. Each branch on the tree represents a split between two or more factors (actions or alternative hypotheses) that account for differences in the outcomes. The left side of each split represents factors that result in lower probabilities of exceeding the survival or recovery threshold; the right side represents factors that produce higher probabilities. The most important factors (those that account for the greatest amount of differences in the results) are split first (at the top), followed by progressively less important factors at the bottom of the diagram. The vertical length of each branch is proportional to the amount of variance explained by each factor, and the number at the bottom of each branch is the average outcome for that combination of factors. The most important factors were assumptions relating to the actions themselves, the passage–transportation models, estuary and ocean survival factors of in-river fish, and regional patterns in estuary and ocean mortality effects.

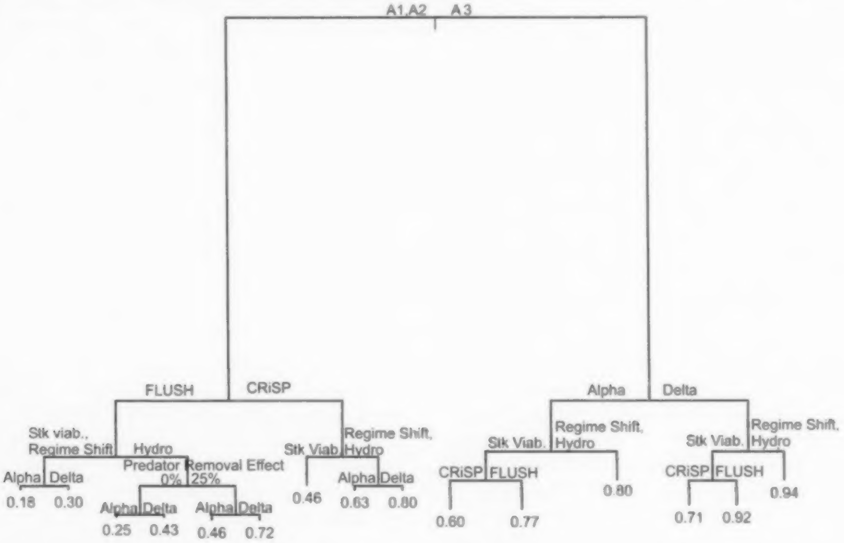
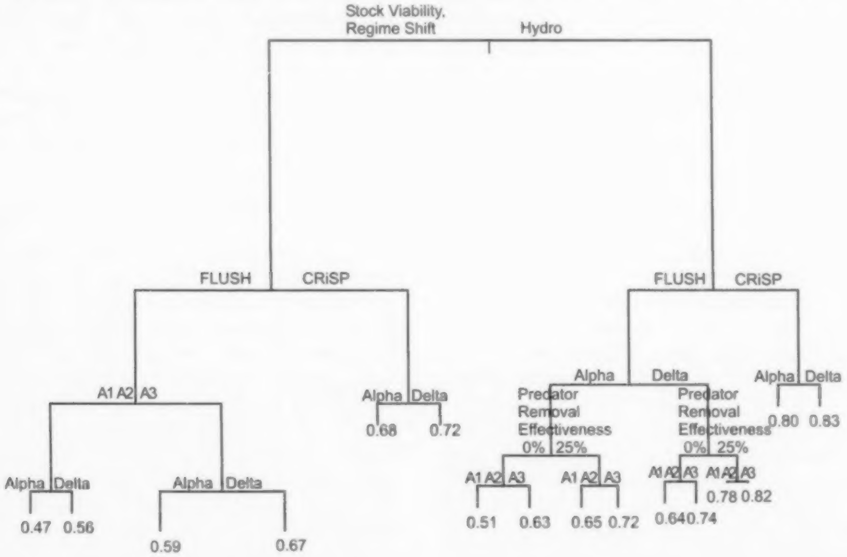

A1,A2
A3
FLUSH
CRiSP
Alpha
Delta
Stk viab., Regime Shift
Hydro
Predator Removal Effect
0%
25%
Stk Viab.
Regime Shift, Hydro
Alpha
Delta
0.18
0.30
Alpha
Delta
Alpha
Delta
0.25
0.43
0.46
0.72
0.46
Alpha
Delta
0.63
0.80
Stk Viab.
Regime Shift, Hydro
CRiSP
FLUSH
0.60
0.77
0.80
Stk Viab.
Regime Shift, Hydro
CRiSP
FLUSH
0.71
0.92
0.94

Fig. 6. Categorical Analytical Regression Tree (CART) diagram showing the relative influence of actions and uncertainties on the probability of exceeding the survival threshold over 24 years. See Fig. 5 for interpretation. The most important factors were the passage–transportation models, estuary and ocean survival factors for in-river fish, and regional patterns in estuary and ocean mortality effects. This CART diagram is truncated for clarity of presentation; if pruned to an R^2 of 0.95, there were 37 splits.


Stock Viability, Regime Shift
Hydro
FLUSH
CRiSP
FLUSH
CRiSP
A1 A2
A3
Alpha
Delta
Alpha
Delta
0.47
0.56
0.59
0.67
Alpha
Delta
0.68
0.72
Alpha
Delta
Predator Removal Effectiveness
0%
25%
A1 A2
A3
A1 A2
A3
0.51
0.63
0.65
0.72
Predator Removal Effectiveness
0%
25%
A1 A2
A3
A1 A2
A3
0.64
0.74
0.78
0.82
Alpha
Delta
0.80
0.83

ably better for fish than conditions have been since 1995. The base periods that we used thus represented more favorable future climate and mortality conditions, and thus produced higher projected numbers of spawners, than what would be expected using only the most recent estimates of common year-effects and total mortality factors. Although

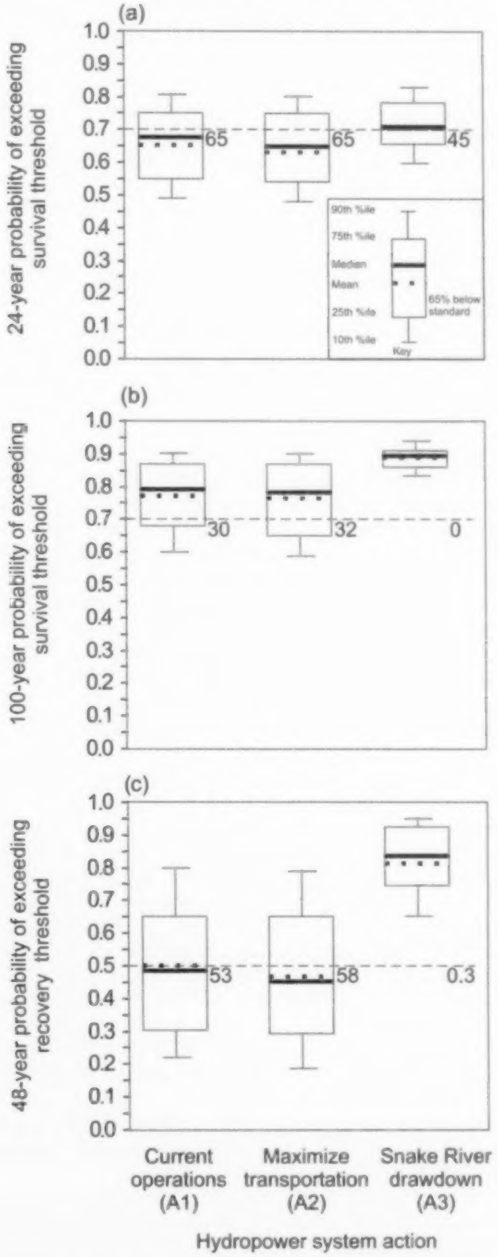


Fig. 7. Distributions of probabilities of exceeding (*a*) the survival threshold over 24 years, (*b*) the survival threshold over 100 years, and (*c*) the recovery threshold over 48 years for the three hydrosystem actions. The figure also shows the mean and median of the distributions and the percentage of outcomes that fell below the standards of 0.7 for survival thresholds and 0.5 for recovery thresholds (these standards are indicated by horizontal broken lines). There were 240 outcomes for actions A1 and A2 and 1920 for A3. Distributions of the 24-year survival metric were similar for the three actions. Over the long term (48 and 100 years), however, A3 tended to produce higher and less variable probabilities of exceeding survival and recovery thresholds than did A1 and A2.

(a)
24-year probability of exceeding survival threshold
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
65
65
45
90th %ile
75th %ile
Median
Mean
25th %ile
10th %ile
65% below standard
Key
(b)
100-year probability of exceeding survival threshold
30
32
0
(c)
48-year probability of exceeding recovery threshold
53
58
0.3
Current operations (A1)
Maximize transportation (A2)
Snake River drawdown (A3)
Hydropower system action

this leads our models to be optimistic, it applies to all actions equally and thus will not affect the relative ranking of actions.

In conclusion, decision analysis provides a useful approach for including a broad range of alternative hypotheses about past and future responses of Snake River spring and summer chinook stocks to environmental and anthropogenic factors, systematically looking at the range of possible effects of recovery actions on these stocks, and assessing how robust each action is to uncertainties. By including these uncertainties, robust recovery strategies can be identified before uncertainties are fully resolved, which may take more time than listed stocks have. The PATH decision analysis showed that uncertainties related to the cause of mortality in the estuary and ocean life stages had the most influence on projected outcomes of actions to recover Snake River spring and summer chinook stocks. These uncertainties are more likely to be resolved by implementing well-designed management experiments than by status quo actions because of limitations in current monitoring approaches for measuring changes in estuary and ocean survival rates. Given that these uncertainties exist, the natural river drawdown option was more risk averse than either continuing current operations or maximizing transportation.

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Appendix. Technical supplement

Calculation of survival and recovery standards

The survival standard was based on the probability that the projected number of spawners of individual stocks will exceed escapement thresholds that are thought to be high enough to avoid extinction. For the seven Snake River spring and summer chinook index stocks, the threshold level was either 150 or 300 spawners, depending on the amount of spawning habitat in spawning streams (the higher threshold was applied to streams where spawners are spread out over a larger area). These values were chosen because below these escapement levels, spawner–recruit relationships are poorly known and unpredictable changes in population behavior (e.g., depensation) are likely to occur. The probability of exceeding the survival threshold for each action was calculated as the fraction of the total number of years simulated (3000 Monte Carlo simulations × number of years in each simulation) in which the projected escapement exceeded the threshold. Two time periods were used: simulation years 1 to 24, to reflect short-term implications of actions, and a 100-year simulation period to reflect long-term effects.

The recovery standard described the ability of a certain hydrosystem action to recover stocks to healthier levels. This standard was based on the probability that the spawning abundance of a stock will be above a specified recovery escapement threshold. For spring and summer chinook stocks, the recovery escapement threshold was calculated as 60% of the pre-1971 brood-year average spawner counts for each stock (thresholds for the seven index stocks ranged from 350 to 1150 spawners). The probability of exceeding the recovery threshold was calculated by first taking the geometric mean spawner abundance over the last 8 years of a 48-year simulation (to dampen the effects of unusual years) and then calculating the fraction of the 3000 Monte Carlo simulations in which that geometric mean exceeded the recovery escapement threshold.

The probabilities of exceeding survival and recovery thresholds were calculated for each of the seven Snake River index stocks of spring and summer chinook. To aggregate these performance measures for individual stocks into a single measure for the entire Snake River spring and summer chinook ESU, NMFS defined an overall jeopardy standard. To meet this standard, an action must result in a "high percentage" of the individual populations having a "high" probability of being above the survival threshold level and a "moderate" probability of being above the recovery level. NMFS defined "high percentage" of stocks as 80% of the index populations. "High" and "moderate" probabilities were informally defined by PATH as 0.7 for the survival threshold and 0.5 for the recovery threshold. Therefore, for an action to meet the overall jeopardy standard, it must result in six out of the seven Snake River index stocks (around 80%) having at least a 0.7 probability of being above the survival threshold and at least a 0.5 probability of being above the recovery threshold. For this reason, we report probabilities of exceeding survival and recovery thresholds only for the sixth best stock.

Transportation assumptions

General approach for estimating D

D is the ratio of the estuary and ocean survival rate of transported fish (λ_t) to estuary and ocean survival rate of in-river (nontransported) fish (λ_n). D was estimated from smolt-to-adult survival rates (SARs) of experimental groups of tagged fish in transportation studies (Ward et al. 1997) using eq. A1:

$$\text{(A1)}\quad D = \frac{\lambda_t}{\lambda_n} = \frac{\text{SAR}_t}{\text{SAR}_n} \cdot \frac{V_c}{V_t} = T{:}C \cdot \frac{V_c}{V_t}$$

where λ_t is the estuary and ocean survival rate of transported fish, λ_n is the estuary and ocean survival rate of in-river fish, SAR_t is the smolt-to-adult survival rate of experimental groups of transported fish from the point of their collection and placement in a truck or barge back to that same point as adults, and SAR_n is the smolt-to-adult survival rate of experimental groups of in-river fish from the point of their collection and re-release back to that same point as adults. The ratio of $\mathrm{SAR}_t{:}\mathrm{SAR}_n$ is known as the transport–control ratio ($T{:}C$). V_t is the survival rate of experimental groups of transported fish in the barge from the top of the hydropower system to below Bonneville Dam (assumed to be 0.98), and V_c is the survival rate of experimental groups of in-river fish from the top of the hydropower system to below Bonneville Dam (obtained from passage models or survival studies).

Transportation hypotheses

The decision analysis incorporated two hypotheses about the relative effect of transportation on survival rates in the estuary and ocean. Each hypothesis was associated with one of the two passage models. The first D hypothesis was implemented in conjunction with the FLUSH passage model. Historical D estimates were derived from a function relating $T{:}C$ to the survival of in-river fish from the tailrace of the collection dam to below Bonneville dam (V_c). $T{:}C$ data for this function came from transport studies conducted at Lower Granite and Little Goose dams in 1971, 1972, 1973, 1975, 1976, 1978, 1979, 1986, and 1989; estimates of V_c were based on per-project expansions of NMFS reach survival studies for these years except 1986 and 1989, when there were no NMFS survival studies (V_c was estimated with the FLUSH passage model in those years). The function was applied to retrospective FLUSH model estimates of V_c from 1977 to 1992 to derive estimates of $T{:}C$, from which annual D values were calculated using eq. A1. These annual values were used in the retrospective modeling. The median V_c value using this approach was 0.26 from 1968–1979 and 0.22 from 1980–1992. Median D values were 0.41 before 1980 and 0.34 from 1980–1992. The $T{:}C$ vs. V_c relationship was also applied prospectively, in conjunction with projected estimates of V_c values under the various management actions, to derive a set of year-specific D values for prospective modeling.

The second D hypothesis was implemented with the CRiSP passage model. In this hypothesis, historical D values were estimated for each transportation study carried out at Lower Granite, Little Goose, Ice Harbor, and McNary dams between 1969 and 1995 using the $T{:}C$ ratio estimated from that study, an estimate of the survival rate of in-river fish (V_c) from the CRiSP passage model, and eq. A1. Median V_c estimates using the CRiSP model were 0.13 before 1980 and 0.34 from 1980 to 1996. The median of the 1969–1979 D values (0.17) was used for retrospective modeling of years 1977–1979 and the median of the 1980–1995 D values (0.63) was used for retrospective modeling of years 1980–1992. For prospective modeling, the life-cycle model selected randomly from D values calculated from the most recent studies (1986, 1989, 1994, and 1995) because they were thought to be most representative of current collection and transport methods.

Mathematical description of life-cycle models

Delta version

The mathematical representation of the Delta version of the life-cycle model was

$$\text{(A2)}\quad \ln(R_{t,i}) = (1+p)\ln(S_{t,i}) + a_i - b_i S_{t,i} - M_{t,i} - \Delta m_t + \delta_t + \varepsilon_{t,i}$$

where $R_{t,i}$ (adult returns to the Columbia River mouth originating from spawning in year t and river sub-basin i) and $S_{t,i}$ (spawners in year t and river sub-basin i) were provided from the run reconstructions (Beamesderfer et al. 1997). $M_{t,i}$ was direct instantaneous passage mortality estimated by the passage models from the head of Lower Granite reservoir to below Bonneville Dam, which depended on year and included combined mortality of both transported and in-river smolts. $M_{t,i}$ varies for downriver stocks but is the same for all sub-basins i within the Snake River sub-region. Estimated parameters in eq. A2 were a_i (Ricker a parameter, inherent stock productivity for sub-basin i), b_i (Ricker b parameter, stock-carrying capacity for sub-basin i), and a depensation parameter (p), which represents a reduction in the number of recruits per spawner as spawner abundance declines and is applied to all stocks. Fits of eq. A2 to the spawner–recruit data generated values of p close to zero, which suggests that there is little evidence for depensation in these data. We also estimated δ_t (common year-effects influencing both Snake River and six Lower Columbia River stocks), $\varepsilon_{t,i}$ (random effects specific to each stock in each year), and Δm_t (extra mortality rate, which depends on year t). "Extra mortality" was any mortality occurring outside the juvenile migration corridor that was not accounted for by the other terms in eq. A2.

The Δm_t term was estimated as

$$\text{(A3)}\quad \Delta m_t = m_{t,i} - M_{t,i}$$

with $M_{t,i}$ defined as above and $m_{t,i}$ defined as

$$\text{(A4)}\quad m_{t,i} = X \cdot n_{t,i} + \mu_t$$

where $n_{t,i}$ is the total number of X-type dams (defined as Bonneville, John Day, and (or) The Dalles) that stock i must pass in year t, X is the dam passage mortality for all X-type dams and years (estimated by the life-cycle model), and μ_t is the incremental total mortality between the Snake River basin and the furthest up-river X dam in year t (also estimated by the life-cycle model).

The estuary and ocean survival rate of in-river fish (λ_n) was estimated retrospectively as

$$\text{(A5)}\quad \lambda_n = \mathrm{e}^{(-m-\ln(\omega))}$$

where m was defined as in eq. A4 and ω (system survival) was defined as the number of in-river equivalent smolts below Bonneville Dam (i.e., adjusting for relative estuary and ocean survival of transported fish) divided by the population at the head of the first reservoir and was calculated as

$$\text{(A6)} \quad \omega = e^{(-M)}(DP_{bt} + 1 - P_{bt})$$

where e^{-M} is the weighted average survival rate of transported and in-river smolts from the top of the Lower Granite reservoir to below Bonneville dam (estimated by the passage models), P_{bt} is the proportion of all smolts arriving below Bonneville Dam that were transported (estimated by the passage models), and D is the estuary and ocean survival rate of transported fish relative to that of in-river fish (estimated by the transportation models; see eq. A1). The Delta version of the life-cycle model thus calculated λ_n as the residual left after factoring the system survival rate (ω) and a common year-effect (δ) from the estimated overall survival rate.

Alpha version

The basic equation for the Alpha version of the life-cycle model was

$$\text{(A7)} \quad \ln(R_{t,i}) = (1 + p)\ln(S_{t,i}) + a_i - b_i S_{t,i} - M_{t,i} - \alpha_{t,j} + \varepsilon_{t,i}$$

where all terms in the Alpha model except $\alpha_{t,j}$ are the same as terms in the Delta model. The $\alpha_{t,j}$ term is the extra mortality in year t for subregion j:

$$\text{(A8)} \quad \alpha_{t,j} = \alpha_n - (\text{average } \alpha_n) - \ln(D_t P_{bt} + 1 - P_{bt}) + (\text{average } \ln(D_t P_{bt} + 1 - P_{bt}))$$

where the averaged terms encompass brood years 1952–1990, $P_{b,t}$ and D_t are defined as in eq. A6, and

$$\text{(A9)} \quad \alpha_n = (c_1 / F_t) + (c_2 E_t / F_t) + \text{STEP}_j$$

where F_t is the average flow (in 1000 ft^3/s) at the mouth of the Columbia River for year t during April and June and E_t is the PAPA drift climate index variable (the latitude of a drifting object after 3 months starting at Ocean Station PAPA in the Northeast Pacific Ocean). The F_t and E_t terms were input to the model. Estimated parameters in eq. A9 were STEP$_j$, which was equal to $-\ln(\lambda_n)$ in the Delta model (see eq. A5) and estimated for brood years after 1974 (assumed to be zero before 1975), and the coefficients c_1 and c_2. The Alpha version of the model thus estimated an estuary and ocean survival factor (STEP) directly as a stepped increase in estuary and ocean mortality after brood year 1974 and then used STEP in conjunction with passage model estimates of passage-related survival and estimated relationships between estuary and ocean survival and various climatic factors to calculate an overall spawner-to-recruit survival rate.

Note that although the Ricker a_i term in the Alpha model was defined and estimated in a similar manner as in the Delta model, it was not directly comparable because of the subtraction of averages in the $\alpha_{t,j}$ term (eq. A8). Adjustment of the Alpha model Ricker a_i term by addition of averages in the $\alpha_{t,j}$ term was necessary to make the Alpha and Delta model Ricker a_i terms comparable.

Comparison of the Delta and Alpha versions

With the definitions below, both the Delta and Alpha versions of the model can be written as a Ricker model with four specially defined terms:

$$\text{(A10)} \quad \ln(R) = (1 + p)\ln(S) + \text{Term1} + \text{Term2} + \text{Term3} + \text{Term4} - bS + \varepsilon$$

where Term1 was the Ricker a value, representing the collection of all constant terms in each model other than those needed to center climate variables modeled as Markov processes. In the Delta model, this was the term "a"; in the Alpha model, this was the term "a – average($\ln(DP_{bt} + 1 - P_{bt})$) + average(STEP)". Term2 was the logarithm of system survival, $\ln(\omega)$. In both models, this was the term "$-M + \ln(DP_{bt} + 1 - P_{bt})$" and was supplied by the passage and transportation models. Term3 was the logarithm of post-Bonneville survival factor of in-river fish, $\ln(\lambda_n)$. In the Delta model, this was the term "$-m - \ln(\omega)$"; in the Alpha model, this was the term "–STEP". Term 4 was represented by Markov-type climate variables, centered so that they sum to zero over brood years 1951–1990. In the Delta model, this was the term δ_t; in the Alpha model, this was the term "$c_1(1/F - \text{average}(1/F)) + c_2(E/F - \text{average}(E/F))$".

Hypotheses for estuary and ocean survival factor for in-river fish (λ_n)

Hydro hypothesis

The Hydro hypothesis postulated that λ_n has been, and will be, related to delayed effects of passage (such as increased stress) through the eight dams of the Federal Columbia River Power System. Evidence for this hypothesis is reviewed in Budy et al. (2002). The Hydro hypothesis was implemented in the life-cycle model by selecting a particular flow year (from 1977 to 1992) based on the frequency of that type of year in the historical (1929–1992) record and then applying eq. A11.

$$\text{(A11)} \quad (1 - \lambda_{n,p}) = (1 - \lambda_{n,r}) \cdot \frac{(1 - V_{n,p})}{(1 - V_{n,r})}$$

where $\lambda_{n,p}$ is the prospective estuary and ocean survival factor for in-river fish for a future year p, a future year with unregulated flow equal to that of a historical flow year r. $\lambda_{n,p}$ was estimated from $\lambda_{n,r}$ (retrospective estuary and ocean survival factor for in-river fish for historical flow year r, calculated in retrospective life-cycle modeling), $V_{n,p}$ (prospective passage survival rate of in-river fish for future flow year p, calculated in prospective passage modeling), and $V_{n,r}$ (retrospective passage survival rate of in-river fish for historical flow year r, calculated in retrospective passage modeling).

Stock viability hypothesis

The stock viability hypothesis proposed that estimates of λ_n for the 1977–1992 period will apply indefinitely in the future, even if hydrosystem direct mortality declines or climate improves. Several mechanisms to account for decreased stock viability were proposed, including an increase in incidence or severity of bacterial kidney disease (BKD) in wild populations resulting from increased numbers of hatchery fish, increased predation rates on juveniles because of low stock sizes, and insufficient nutrients from returning adults' carcasses to support the growth of parr. The key feature of this hypothesis was that future hydrosystem actions, even if they improved survival rates through the hydropower system, would have no effect on estuary and ocean survival rates of in-river fish. The stock viability hypothesis was implemented in the life-cycle model by selecting (in each simulation and year) a particular flow year (from 1977 to 1992) based on the frequency of that type of year in the historical (1929–1992) record and then setting the prospective value of λ_n equal to the retrospective value for that flow year.

Regime shift hypothesis

The regime shift hypothesis suggested that the estuary and ocean survival factor for in-river fish was due to a long-term (60-year) cycle in ocean climate. This regime is believed to have shifted from good to poor during brood year 1975 and is expected to return to above-average conditions in 2005 (Beamish et al. 1999). Key assumptions in this hypothesis were that cyclical changes in climate affect salmon production (Hare et al. 1999) and that these climatic effects on Snake River stocks are systematically different from effects on lower Columbia River stocks.

In the life-cycle model, the regime shift hypothesis was implemented by selecting a flow year from the historical period according to the phase of the 60-year climatic cycle. For forward simulation years up to 2005, flow years were selected from the "bad" phase of the cycle (1975–1990). From simulation years 2006 to 2035, flow years were selected from a period of good ocean conditions (1952–1974). For each selected flow year, the prospective value of λ_n was assumed to be the same as the retrospective value estimated for that flow year.

Application of decision analysis to evaluate recovery actions for threatened Snake River fall chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: We used models and decision analysis to incorporate uncertainties into evaluations of two recovery actions for Snake River fall chinook salmon (*Oncorhynchus tshawytscha*): (*i*) maximize transportation and (*ii*) natural river drawdown of four lower Snake River dams. In the retrospective analysis, we compared alternative stock–recruit models and selected one that was consistent with historical spawner–recruit data and allowed us to implement alternative hypotheses about hydrosystem, hatchery, harvest, and environmental effects. In the prospective analysis, we used this model and posterior distributions of its parameters in a decision analysis framework to compare projected escapements for the two actions over a range of alternative hypotheses. We found that drawdown was most risk averse, producing larger long-term escapements than maximizing transportation under most hypotheses and model assumptions. Maximizing transportation and drawdown produced similar escapements only if we assumed high or increasing estuary and ocean survival rates of transported fish coupled with either severe reductions in harvest rates or insensitivity of upstream survival rates to dam construction and removal. Although there was relatively little information available for Snake River fall chinook (particularly about estuary and ocean survival rates of transported smolts), decision analysis was a useful technique for organizing data, assessing actions over a range of uncertainties, and identifying research priorities.

Résumé : Des modèles et une analyse décisionnelle nous ont permis d'incorporer les incertitudes dans l'évaluation de deux stratégies de récupération des populations automnales des Saumons quinnat (*Oncorhynchus tshawytscha*) de la rivière Snake, soit de maximiser le transport des saumoneaux, soit de faire baisser les eaux de la rivière à leur niveau naturel à quatre barrages du bassin inférieur. Dans une analyse rétrospective, nous avons comparé divers modèles de stock–recrutement de rechange et en avons choisi un qui correspondait aux données historiques sur les géniteurs et les recrues et qui nous permettait d'avancer diverses hypothèses sur les effets de l'hydrosystème, de la pisciculture, de la récolte et de l'environnement. Dans notre analyse prospective, ce modèle et les distributions a posteriori de ses paramètres nous ont permis de comparer, dans le cadre d'une analyse décisionnelle, les échappées prédites pour chacune des stratégies dans une gamme d'hypothèses de rechange. Nous avons trouvé que la baisse du niveau était la stratégie qui posait le moins de risques; elle produisait aussi à long terme des échappées plus fortes que l'augmentation du transport sous la plupart des hypothèses et des présuppositions du modèle. La maximisation du transport et la baisse du niveau donnaient des échappées semblables seulement si on présupposait que les poissons transportés avaient une survie élevée ou plus grande dans l'estuaire et l'océan; il fallait aussi qu'il y ait une réduction importante des taux de récolte ou alors que les taux de survie en amont ne soient pas affectés par la construction ou le retrait des barrages. Bien qu'il y ait eu relativement peu de renseignements disponibles sur la population automnale des Saumons quinnat de la rivière Snake (en particulier sur les taux de survie en estuaire et en océan des saumoneaux transportés), l'analyse décisionnelle s'est avérée utile pour organiser les données, évaluer les stratégies dans une gamme d'incertitudes et identifier les priorités de recherche.

[Traduit par la Rédaction]

Introduction

The Plan for Analyzing and Testing Hypotheses (PATH) was a multiagency research program to resolve biological uncertainties about recovery of chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) stocks in the Snake River sub-basin of the Columbia River (Marmorek and Peters 2001). PATH grew out of a review of three modeling systems (Barnthouse 1993) and a subsequent assessment by the National Marine Fisheries Service (NMFS 1995). Both documents recommended examining the models' underlying hypotheses. PATH's objectives were to ex-

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amine these hypotheses in a rigorous but collaborative manner, resolve as many differences as possible, and evaluate alternative actions in the light of remaining uncertainties.

There were two phases of PATH analyses. "Retrospective analyses" formulated hypotheses and assessed their consistency with historical data sets. Available data were sufficient to resolve only some uncertainties about the effects of alternative actions and environmental factors on survival rates. Remaining uncertainties were carried forward in "prospective analyses", which used models of Snake River salmon to project escapements resulting from alternative recovery actions. We used decision analysis as a framework for systematically incorporating uncertainties into the evaluation of alternative recovery actions (Peterman and Anderson 1999). This provided a mechanism for determining the relative influence of various sources of uncertainty on the outcomes of alternative actions and identifying risk-averse recovery actions that performed well over a range of uncertainties. PATH completed retrospective and prospective analyses of Snake River spring- and summer-run chinook (Deriso et al. 2001; Peters and Marmorek 2001) and ocean type (juveniles spend <1 year in freshwater) fall-run chinook (this study).

Analyses of fall chinook were less detailed than spring and summer chinook because there were less data. For spring and summer chinook, we had 33–38 years of spawner–recruit data for seven Snake River and three lower Columbia River stocks, numerous transportation studies conducted between 1968 and 1995, and 19 years of juvenile and smolt-to-adult survival rate estimates between 1966 and 1996. In contrast, for fall chinook, we had 20–27 years of spawner–recruit data for only three stocks and 4 years of juvenile survival data (all from recent years). In addition, sample sizes have been too small to produce reliable data for evaluating the benefits of transportation for Snake River fall chinook. The lack of data for fall chinook tested the utility of our decision analysis methods under conditions of high uncertainty.

Methods

Description of stocks

PATH reconstructed spawner and recruit information for three fall chinook stocks in the Columbia Basin (Fig. 1; Table 1). The Snake River population (the focus of this study) consists of adult fall chinook spawning between Hells Canyon and Lower Granite dams. The proportion of spawners of hatchery origin (hatchery fraction) has been substantial since 1990. After rearing in the mainstem of the Snake River, juveniles migrate through eight dams on the Snake and Columbia rivers or are collected at upper dams and transported by truck to below Bonneville Dam. Hatchery fractions, survival rates through the hydrosystem, and proportion transported are summarized in Table 1. Adult fish experience ocean and in-river harvest rates of around 30% and interdam losses during upstream migration of 40–50%.

Retrospective analysis

The purpose of the retrospective analysis was to identify a model structure for prospective analyses, a set of hypotheses to be carried forward into the prospective analyses, and a distribution of parameter values consistent with the spawner–recruit data. Spawner–recruit survival anomalies for Snake River fall chinook (residuals from predicted recruits per spawner using a standard Ricker (1975) spawner–recruit model) declined starting in the early 1980s (Fig. 2). This period was characterized by full operation of the Snake River dams, increasing transportation of smolts, and increased proportion of hatchery fish in the spawning population (Peters et al. 1999).

We explored the effects of these and other mortality factors on observed survival rates of Snake River fall chinook using passage and life-cycle models (Fig. 3). Passage models computed the total direct in-river and transport mortality (M) of Snake River smolts through the eight dams of the Federal Columbia River Power System and the proportion of smolts arriving below Bonneville Dam that were transported (P_{bt}). Values were generated for brood years 1964 to 1991 (Table 1), based on assumptions about migration timing, survival rates in free-flowing reaches, predation rates, bypass, turbine, spillway, and transport mortality, temperature effects, fish travel time, and effectiveness of predator-removal programs (see Peters et al. (1999) for details). M and P_{bt} were assumed to be calculated without error.

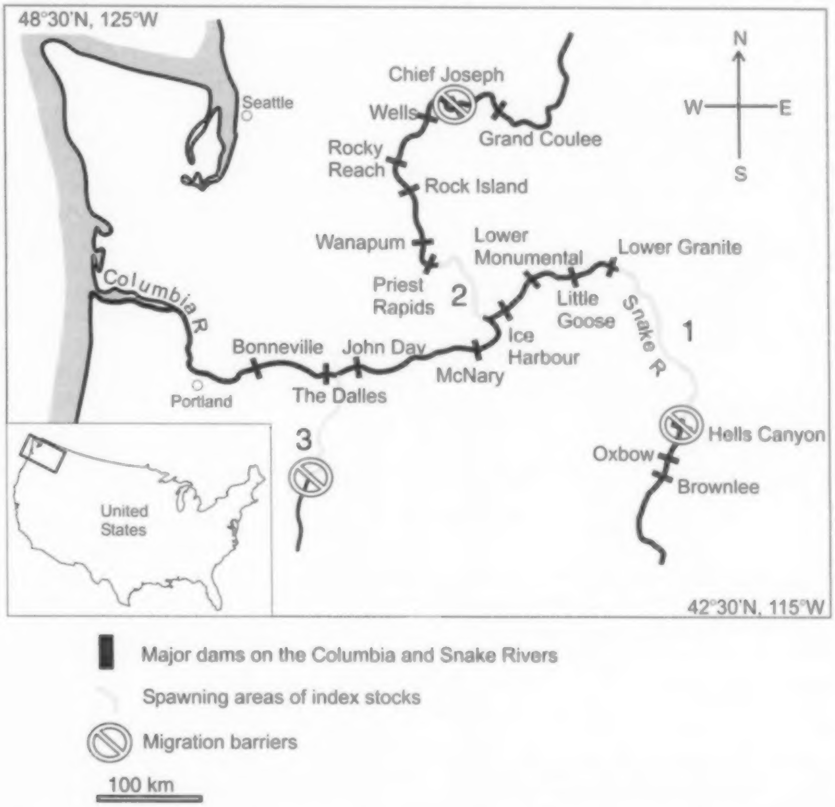
Survival of Snake River fall chinook through the spawning, rearing, and adult life stages was modeled with a generalized Ricker spawner–recruit model:

$$(1)\qquad R_t = (S_{\mathrm{wild}_t} + E \cdot S_{\mathrm{other}_t})^{(1+p)}\mathrm{e}^{a}\mathrm{e}^{-b(S_{\mathrm{wild}_t} + E \cdot S_{\mathrm{other}_t})}\mathrm{e}^{-M_t} \times (DP_{bt} + 1 - P_{bt})\mathrm{e}^{\mathrm{clim}}\mathrm{e}^{-\mathrm{STEP}}\mathrm{e}^{e_t}$$

where M_t and P_{bt} were computed by passage models, and R_t (number of returns to the Columbia River in the absence of ocean harvest), S_{wild_t} (number of wild age-3+ spawners in year t), and S_{other_t} (number of hatchery spawners in year t) were obtained from run reconstructions (Table 1). S_{wild_t} and S_{other_t} were assumed to be measured without error, based on the insensitivity of PATH's spring and summer chinook model to spawner measurement error (Deriso et al. 2001). Estimated parameters in eq. 1 were the Ricker a and b parameters, a depensation parameter (p) to reflect potential changes in survival at low spawner abundance, a climate factor accounting for mortality sources other than those specified by other parameters in the model (clim), and overall residual variation in the Snake River stock in year t (e_t). Both measurement error in the returns (R_t) and process error (natural variation) contributed to the error term e_t. D was the ratio of post-Bonneville (estuary and ocean) survival rate of transported smolts to post-Bonneville survival rate of nontransported smolts (i.e., if $D < 1$, transported fish have lower post-Bonneville survival rates than nontransported fish). D was assumed to be a constant during all years of transportation and was either specified or estimated. STEP represented the average increase in overall mortality after accounting for the hypothesized delayed effects of transportation (D) and total direct passage mortality (M_t). This increase in overall mortality occurred in either brood year 1970 (presumed to be related to the construction and start-up of the four lower Snake River dams) or in 1976 (presumed to be related to changes in ocean conditions or to the start of full operation of the four lower Snake River dams). We also estimated a parameter to represent relative spawning effectiveness of hatchery fish (E), ranging from 0 (hatchery spawners made no contribution to future generations) to 1 (hatchery spawners made the same contribution as wild fish).

We explored 30 variations in the structure of eq. 1 representing alternative hypotheses about the effects of various mortality factors, and evaluated their consistency with the historical spawner–recruit data (Table 2). All 30 variations omitted the depensation parameter p because we found that the estimated value of this parameter was always close to zero, indicating no evidence for depensatory effects in the spawner–recruit data. Variations varied in (*i*) complexity (from simple two-parameter Ricker models to complex Ricker models such as eq. 1); (*ii*) passage models (either CRiSP (Columbia River Salmon Passage), developed by researchers at the University of Washington, or Fall FLUSH (Fish Leaving Under Several Hypotheses), developed by scientists at State and

Fig. 1. Location of fall chinook index populations: 1 = Snake River (fish pass through eight mainstem dams); 2 = Hanford Reach (4 dams); 3 = Deschutes River (2 dams). Approximate latitude and longitude are given in the corner of the diagram.


48°30'N, 125°W
Seattle
Chief Joseph
Wells
Grand Coulee
Rocky Reach
Rock Island
Wanapum
Priest Rapids
2
Lower Monumental
Lower Granite
Little Goose
Snake R
1
Ice Harbour
McNary
Columbia R
Bonneville
John Day
The Dalles
Portland
3
Hells Canyon
Oxbow
Brownlee
United States
42°30'N, 115°W
N
W
E
S
Major dams on the Columbia and Snake Rivers
Spawning areas of index stocks
Migration barriers
100 km

Tribal fisheries agencies); and (*iii*) years in which STEP takes effect (either 1970 or 1976). Some models estimated *D* and *E*, whereas others treated these parameters as fixed inputs. The model variations also included several indirect approaches for estimating annual climate factors because there were insufficient degrees of freedom in the spawner–recruit data to estimate these directly. Approaches ranged from omitting the climate factor entirely to using residuals from a Ricker model fit to the Hanford or Deschutes fall chinook data. In models that used Deschutes residuals, we used the significant positive correlation between Deschutes and Snake residuals ($r = 0.75$) to reduce the residual error in eq. 1:

$$(2) \qquad e_t = g \cdot e_t(\text{des}) + e_t'$$

where e_t(des) represents residual variation in Deschutes stock in year t (estimated from fitting a standard Ricker stock–recruit model to Deschutes spawner–recruit data), g is the covariation coefficient (estimated), and e_t' is the remaining residual variation in Snake River stock after correlation with Deschutes stock has been removed. This assumed that e_t(des) and e_t' were independent normal random variables. In models that adopted this structure, the climate factor in eq. 1 (clim) dropped out and was absorbed into the e_t term.

We first compared the 30 models to spawner–recruit data and then estimated a distribution of parameter values for selected models. Both the model comparison and parameter estimation analyses were based on the unnormalized posterior density function:

$$(3) \qquad \Pr(\{e_t(\text{des})\}) \cdot \Pr(\{e_t'\}) \cdot \Pr(\text{priors})$$

where the first two terms represent the likelihood functions associated with the Deschutes and Snake River recruitment data, respectively (Gelman et al. 1995; Quinn and Deriso 1999). This involved simultaneous fitting of Ricker-type models to the Deschutes and Snake River stocks. The last term represented the prior distribution for the model parameters. We assumed uniform prior distributions for all parameters, except for the Snake River Ricker *b* coefficient. For this parameter, we assumed a prior distribution

$$(4) \qquad \ln(b) \sim N(\ln(1/5000), 0.25)$$

based on an independent analysis that suggested recruitment was maximized at 5000 spawners (Schaller and Cooney 1992; see McAllister and Kirkwood (1998) for a review of the use of priors in fisheries). Model fits to spawner–recruit data were insensitive to this assumption.

To compare the models to spawner–recruit data, we first calculated the mode of eq. 3 for each model by maximizing that function with respect to unknown parameters. Likelihoods for each of the alternative models were then compared using the Akaike Information Criterion (AIC) and Bayes Information Criterion (BIC), which are essentially penalized versions of the likelihood ratio method (Kass and Raftery 1995; Fournier et al. 1998). Models with lower AIC and BIC scores fit the data better than models with higher scores, and as a general guideline, we considered two models to be "significantly" different when the difference in their AIC or BIC scores was >2. For example, the fit of model 1 (AIC = 49.03) was deemed to be significantly different from model 2 (AIC = 59.48) because the difference in their AIC scores was >2, and the lower AIC score of model 1 suggested a better fit to the

Table 1. Spawner (S) and recruit (R) data for Snake River, Hanford Reach, and Deschutes River fall chinook stocks, brood years 1964–1999 (Deschutes data start in brood year 1977).

	Snake River					Hanford Reach		Deschutes River	
Brood year	S	R	H_{frac}	e^{-M}	P_{bt}	S	R	S	R
1964	7 648	35 240	0.00	0.47	0.00	22 703	100 043	—	—
1965	6 339	62 471	0.00	0.43	0.00	26 668	239 681	—	—
1966	8 623	34 329	0.00	0.46	0.00	29 724	193 231	—	—
1967	10 414	71 436	0.00	0.38	0.00	24 638	307 471	—	—
1968	17 556	48 681	0.00	0.31	0.00	24 035	263 670	—	—
1969	4 649	35 129	0.00	0.25	0.00	28 937	286 328	—	—
1970	4 353	43 363	0.00	0.27	0.00	20 511	590 130	—	—
1971	4 091	22 699	0.00	0.27	0.00	26 393	471 622	—	—
1972	1 371	17 390	0.00	0.20	0.00	19 327	361 190	—	—
1973	2 194	15 716	0.00	0.27	0.00	36 343	398 212	—	—
1974	668	12 910	0.00	0.21	0.00	28 940	333 580	—	—
1975	1 387	10 619	0.00	0.22	0.00	34 628	268 136	—	—
1976	691	7 019	0.00	0.16	0.23	39 987	108 581	—	—
1977	1 011	9 259	0.00	0.22	0.21	40 745	107 827	6414	17 641
1978	841	4 946	0.00	0.20	0.33	21 644	56 563	4099	16 172
1979	802	11 657	0.00	0.26	0.45	24 840	164 027	3728	15 831
1980	515	7 817	0.00	0.37	0.69	21 224	304 686	2788	15 490
1981	878	4 746	0.00	0.35	0.58	14 213	265 436	4704	17 145
1982	1 209	7 500	0.00	0.37	0.67	22 598	458 905	5176	15 725
1983	909	8 723	0.07	0.39	0.65	37 038	647 038	4160	16 090
1984	717	9 721	0.23	0.37	0.76	48 149	956 878	2690	56 348
1985	1 080	4 821	0.18	0.35	0.74	71 732	274 308	6333	11 974
1986	1 403	4 971	0.24	0.35	0.81	100 626	239 529	6045	11 576
1987	1 064	2 171	0.57	0.37	0.80	105 347	101 086	6278	4 125
1988	702	3 748	0.29	0.34	0.72	96 329	96 391	7903	8 804
1989	815	2 031	0.49	0.39	0.79	72 022	151 284	3927	10 043
1990	273	975	0.77	0.67	0.93	47 856	131 271	2320	14 416
1991	767	717	0.34	0.66	0.96	37 580	38 067	3684	5 765
1992	674	—	0.17	—	—	34 371	—	3454	—
1993	883	—	0.21	—	—	35 322	—	6126	—
1994	448	—	0.32	—	—	54 373	—	6025	—
1995	226	—	0.43	—	—	39 936	—	6603	—
1996	964	—	0.35	—	—	38 443	—	7734	—

Note: Spawner estimates are the total of natural and hatchery-origin spawners. Recruits are the number of adults at the mouth of the Columbia River that would have been produced by the spawners in a particular brood year in the absence of ocean harvest. Recruits were back-calculated from spawner data using historical estimates of upstream survival rates, in-river harvest rates, and maturity schedules. H_{frac}, fraction of spawners that were of hatchery origin; e^{-M}, weighted average survival rate of transported and in-river fish through the hydropower system; P_{bt}, fraction of fish below Bonneville Dam that were transported. P_{bt} and e^{-M} are the average of CRiSP (Columbia River Salmon Passage) and fall FLUSH (Fish Leaving Under Several Hypotheses) passage model estimates.

data than that of model 2. We then numerically sampled parameters in our selected models using a Monte Carlo Markov Chain algorithm (Gelman et al. 1995) to get parameter distributions for the prospective analysis. Further Monte Carlo analyses revealed only a small bias in our estimates of Ricker a, Ricker b, p, D, and E (Hinrichsen 2001).

Prospective and decision analysis

Alternative actions to be evaluated

The decision analysis focused on two recovery actions related to the operation of the Columbia River hydropower system. In action A2 (or "maximize transportation"), the system is operated to collect as many juvenile fish as possible at the uppermost dams for transport by truck to below Bonneville Dam. This was equivalent to a "status quo" action because the system is currently operated to maximize transportation of fall chinook smolts. Action A3 was natural river drawdown of the four dams on the lower Snake River. With this action, passage around these dams would be restored by removing earthen berms adjacent to the dam structures. Navigation, power generation, and collection of smolts for transportation would be eliminated at these projects.

Performance measures to evaluate the actions

PATH used the jeopardy standards largely accepted by NMFS for Snake River chinook salmon (NMFS 1995) as our primary performance measure (see Peters and Marmorek (2001) for details). The standards were based on the probability (calculated over multiple Monte Carlo simulations) that projected escapement of natural origin spawners would exceed survival and recovery thresholds, which for Snake River fall chinook were 300 and 2500 spawners, respectively. Probabilities of exceeding the survival threshold of 300 spawners were calculated over simulation years 1–24 and 1–100 to capture short- and long-term effects; the probability of exceeding the recovery threshold was calculated over simulation years 41–48.

Fig. 2. Survival anomaly index for Snake River (solid squares), Hanford Reach (open triangles), and Deschutes River (open circles) fall chinook. Annual survival anomalies are the residuals from ln(R/S) predicted from the estimated Ricker stock–recruit curve. Negative values indicate lower survival rates than the average over the entire period.

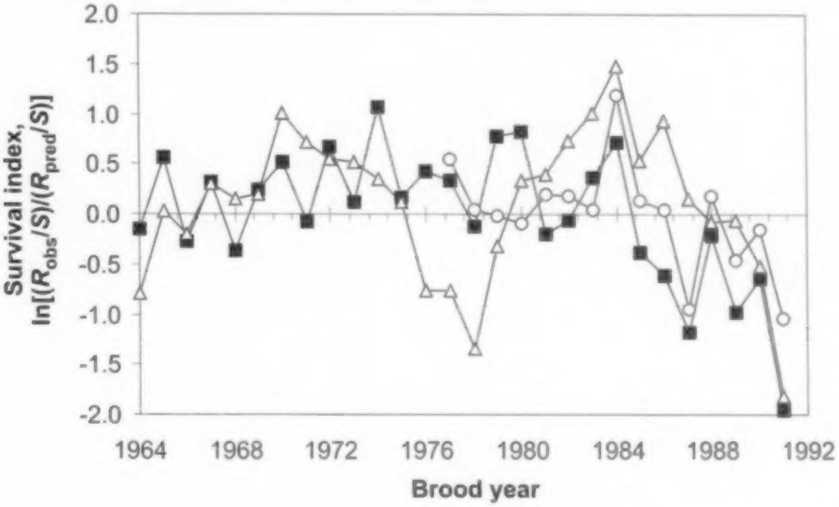
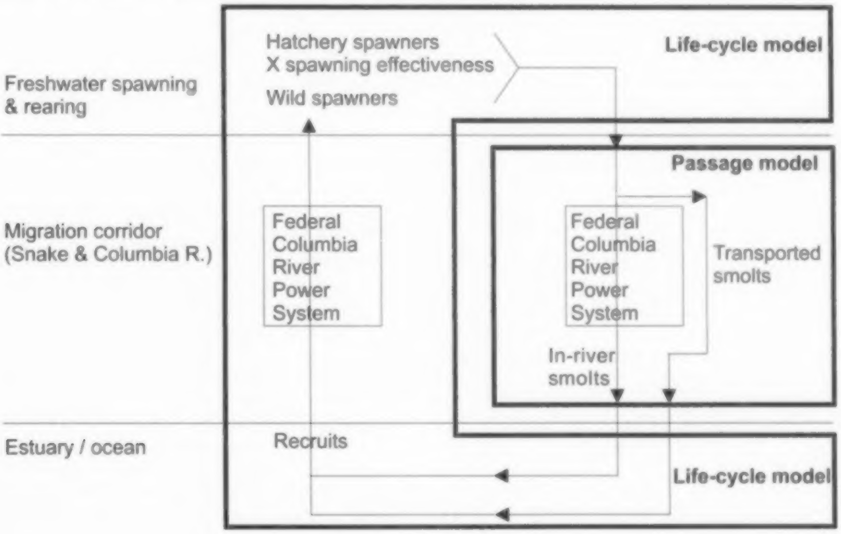


Fig. 3. Schematic of the life cycle of Snake River fall chinook salmon. Passage models estimated survival of smolts in the Columbia and Snake rivers as they pass through (in-river smolts) or around (transported smolts) the Federal Columbia River Power System (FCRPS). Life-cycle models estimated survival rates over the rest of the life cycle.


Freshwater spawning & rearing
Hatchery spawners
X spawning effectiveness
Wild spawners
Life-cycle model
Passage model
Migration corridor (Snake & Columbia R.)
Federal Columbia River Power System
Federal Columbia River Power System
Transported smolts
In-river smolts
Estuary / ocean
Recruits
Life-cycle model

Models to project outcomes of actions

The prospective modeling framework included hydro-regulation, passage, and life-cycle models (Fig. 4). The U.S. Army Corps of Engineers' HYSER hydro-regulation model translated each action into 18 sets of mean monthly flows in the Snake and Columbia rivers (one for each year from 1976 to 1993). Passage models projected annual values for the two passage-related parameters (M, P_{bt}) for each action and for each of the 18 sets of flows that were expected from that action. For example, passage-related parameters generated from the 1988 mean monthly flows represented the expected passage-related survival rates if a given action were implemented and if 1988 natural flow conditions occurred.

The prospective life-cycle model projected the effects of future alternative management actions on spawning escapement of Snake River fall chinook using posterior distributions of model parameters from the retrospective modeling (i.e., Ricker a and b, E, g, climate factor, and either D or STEP) and assumptions about passage survival, ocean and in-river harvest, upstream survival rates, hatchery supplementation, and carrying capacity of spawning habitat under drawdown (Peters et al. 1999). The life-cycle model performed 4000 Monte Carlo simulations of spawning abundance of the Snake River fall chinook stock over 100 years, beginning with brood year 1997. Each simulation drew from the posterior distribution of parameters, as well as a particular "flow year" from 1976 to

Table 2. Combinations of model assumptions compared in retrospective analysis of life-cycle models.

Model	Passage model	Climate factor	E	D	STEP year	STEP	No. of pars	AIC	BIC
1	CRiSP	Deschutes–Snake[a]	0.77	0.03	1970	0.02	6	49.03	57.02
2	CRiSP	None	1.00	0.00	1970	0.00	5	59.48	66.14
3	CRiSP	None	0.13	0.14*	1970	0.08	4	61.52	66.85
4	CRiSP	None	0.00	0.37*	1970	0.00	4	68.72	74.05
5	CRiSP	Ocean Temp.[b]	0.64	0.00	1970	0.00	6	59.64	67.64
6	CRiSP	Spring–summer δ[c]	0.55	0.01	1970	0.00	6	59.55	67.54
7	CRiSP	PAPA index[d]	0.58	0.00	1970	0.00	6	60.43	68.42
8	CRiSP	Hanford[e]	0.55	0.03	1970	0.16	6	55.76	63.75
9	CRiSP	Deschutes–Snake	0.17	0.37*	1976	0.37	5	55.02	61.68
10	CRiSP	Deschutes–Snake	0.00*	0.17	1970	0.09	5	54.07	60.73
11	CRiSP	Deschutes–Snake	0.70*	0.03	1970	0.02	5	47.08	53.75
12	CRiSP	Deschutes–Snake	1.00*	0.02	1970	0.03	5	47.17	53.84
13	FLUSH	Deschutes–Snake	0.87	0.03	1970	0.00	6	56.21	64.21
14	FLUSH	None	1.00	0.00	1970	0.00	5	62.81	69.47
15	FLUSH	None	0.06	0.14*	1970	0.00	4	66.29	71.62
16	FLUSH	None	0.00	0.37*	1970	0.00	4	74.24	79.56
17	FLUSH	Ocean Temp.	0.85	0.00	1970	0.00	6	64.45	72.44
18	FLUSH	Spring–Summer	0.82	0.00	1970	0.00	6	64.35	72.34
19	FLUSH	PAPA index	0.73	0.00	1970	0.00	6	64.10	72.09
20	FLUSH	Hanford	0.64	0.02	1970	0.00	6	62.55	70.54
21	FLUSH	Deschutes–Snake	0.08	0.37*	1976	0.35	5	63.16	69.82
22	FLUSH	Deschutes–Snake	0.00*	0.12	1970	0.00	5	59.47	66.13
23	FLUSH	Deschutes–Snake	0.70*	0.04	1970	0.00	5	54.32	60.98
24	FLUSH	Deschutes–Snake	1.00*	0.02	1970	0.00	5	54.24	60.90
25	None	None	1.00*	NA	NA	No STEP	2	73.63	76.30
26	None	Deschutes–Snake	0.12	NA	NA	No STEP	4	51.21	56.54
27	None	Deschutes–Snake	0.14	NA	1970	–0.47	5	53.18	59.84
28	None	Deschutes–Snake	0.24	NA	1976	–0.58	5	49.40	56.00
29	CRiSP WTT[f]	Deschutes–Snake	0.64	NA	NA	No STEP	6	47.29	55.29
30	FLUSH WTT[f]	Deschutes–Snake	0.67	NA	NA	No STEP	6	46.31	54.31

Note: E, spawning effectiveness of hatchery fish; D, ratio of post-Bonneville survival of transported fish to post-Bonneville survival of in-river (nontransported) fish; * after number in E and D columns indicates that value is fixed; pars, Snake River parameters estimated. AIC (Akaike Information Criterion) and BIC (Bayes Information Criterion) are measures of the fit of the model to the historical spawner–recruit data. Lower AIC and BIC scores indicate better fits to the data; differences in AIC and BIC > 2 represent significant differences in model fit. CRiSP, Columbia River Salmon Passage; FLUSH, Fish Leaving Under Several Hypotheses; WTT, water travel time, the seasonal average number of days that it takes water to flow from Lower Granite Dam to Bonneville Dam; NA, not applicable.

[a] Joint Snake and Deschutes residuals resulting from simultaneous fitting of Ricker stock–recruit models to both stocks.

[b] Ocean temperature index (Hyun 1996) based on average sea surface temperature during the period of October–January at five coastal Canadian weather stations (Langara Is., Cape St. James, Pine Island, Kains Is., and Amphitrite Point).

[c] Maximum likelihood estimates of year-effects (δ) from the spring–summer chinook data (Deriso et al. 2001).

[d] Latitude of a drifting object 3 months after release from Ocean Station PAPA in the Northeast Pacific Ocean.

[e] Residuals from a simple two-parameter Ricker model fit to Hanford spawner–recruit data.

[f] These models replaced CRiSP and FLUSH estimates of M and P_{bt} with passage model estimates of the proportion of fish arriving at Lower Granite Dam that were transported and the water travel time (WTT).

1993 based on the representation of those years in the historical record (1929–1993). The selected flow year determined which of the 18 sets of passage-related parameters were used in that simulation year.

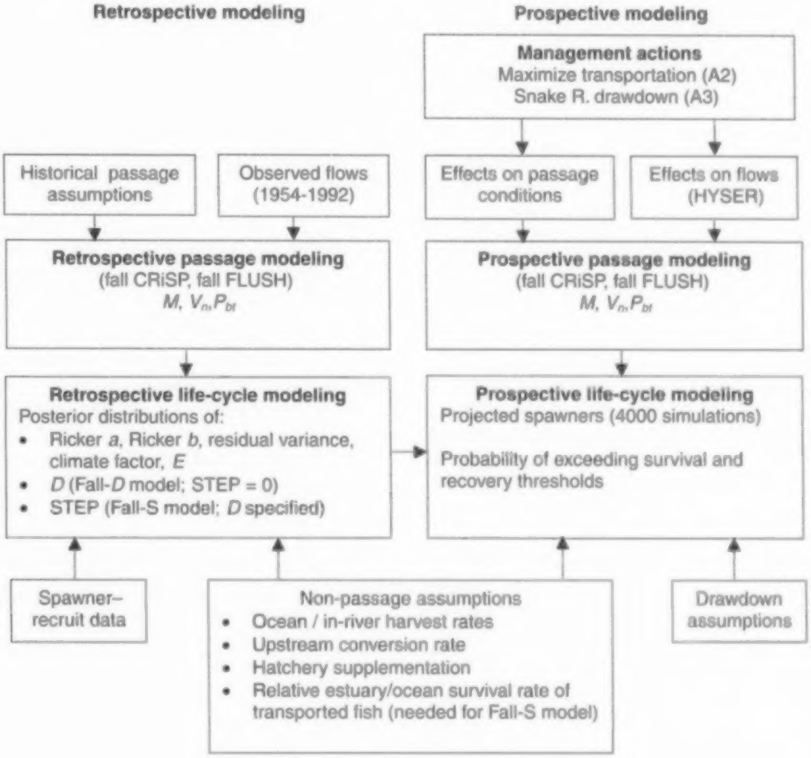
Uncertainties that determine the range of possible outcomes for each action

We included two types of uncertainties in the decision analysis framework. Uncertainty in life-cycle model parameters was included through Monte Carlo simulations (described above). PATH scientists also included discrete alternative hypotheses for six other uncertainties (Table 3; Peters et al. 1999). These uncertainties were selected either because they were important in the spring and summer chinook decision analysis, because the retrospective analysis of fall chinook revealed considerable uncertainty, or because they were related to future conditions and thus not addressed by retrospective analyses.

Juvenile passage survival—Assumptions about factors affecting the survival rate of smolts through the hydropower system (e.g., effects of temperature on mortality rate, the length of time that it takes fish to travel through the hydrosystem, partitioning of in-river survival between dam and reservoir survival, and the proportion of smolts transported) were embodied in the two passage models, fall CRiSP and fall FLUSH. The passage models generated deterministic predictions of total direct passage mortality (M) and proportion transported (P_{bt}).

Relative post-Bonneville survival of transported smolts—The relative survival rates of transported smolts in the estuary and ocean (D) are generally estimated from transportation studies which com-

Fig. 4. Modeling approach used in the decision analysis. Retrospective modeling (left side) described historical patterns in spawner-to-recruit survival rates and estimated distributions of parameters, which were passed to the prospective analysis (right side of diagram). Prospective analyses combined retrospective results with future assumptions to forecast spawning escapements under a range of actions, assumptions, and hypotheses. See text for definition of terms.


Retrospective modeling
Prospective modeling
Management actions
Maximize transportation (A2)
Snake R. drawdown (A3)
Historical passage assumptions
Observed flows (1954-1992)
Effects on passage conditions
Effects on flows (HYSER)
Retrospective passage modeling
(fall CRiSP, fall FLUSH)
M, V_n, P_{bt}
Prospective passage modeling
(fall CRiSP, fall FLUSH)
M, V_n, P_{bt}
Retrospective life-cycle modeling
Posterior distributions of:
• Ricker a, Ricker b, residual variance, climate factor, E
• D (Fall-D model; STEP = 0)
• STEP (Fall-S model; D specified)
Prospective life-cycle modeling
Projected spawners (4000 simulations)
Probability of exceeding survival and recovery thresholds
Spawner–recruit data
Non-passage assumptions
• Ocean / in-river harvest rates
• Upstream conversion rate
• Hatchery supplementation
• Relative estuary/ocean survival rate of transported fish (needed for Fall-S model)
Drawdown assumptions

pare smolt-to-adult survival rates (SAR) of transported and nontransported groups of PIT-tagged (passive induced transponder) fish. Past and current D values for Snake River fall chinook were highly uncertain because there were only 2 years of limited SAR data (1995 and 1996) and because transport methods have changed between the retrospective (brood years 1964–1991) and prospective (post-1991) periods. We implemented four D hypotheses, each consisting of a hypothesized retrospective and prospective D value.

Post-Bonneville mortality (STEP)—STEP was assumed to be zero prior to 1976; afterwards, it was assumed to take on the value of the estimated change in productivity not accounted for by the total direct passage mortality (M) and the effectiveness of transportation (D) from brood years 1976–1991. The interaction between D and STEP led to two model forms for use in prospective modeling. In one version ("Fall-D model"), D was estimated from the spawner–recruit data (as in hypotheses D1 and D3 in Table 3) and STEP was set to zero. In the other form ("Fall-S"), D was specified as a fixed input value and STEP was estimated. In the Fall-S model, we implemented three alternative hypotheses about how estimated STEP values were applied in future simulations. The rationale for the two model forms is described more fully in the retrospective results section below.

Duration of pre-removal period (drawdown action only)—There may be delays in initiating drawdown once such a decision is made because of the Congressional appropriations process and the possibility of litigation.

Juvenile survival rate after drawdown (drawdown action only)—We considered two hypotheses about juvenile survival rates in the 222-km unimpounded reach that would be created by drawdown, based on two analyses of survival rate data collected in a free-flowing reach of the Snake River above Lower Granite Reservoir in 1995, 1997, and 1998. These analyses suggested post-drawdown survival rates of juveniles through the Snake and Columbia rivers (with only four dams remaining) of 0.3 to 0.51, depending on the assumptions used in the analysis and the passage model used to calculate survival through the four remaining dams. Current in-river survival rates through the existing eight dams averaged 0.29 with CRiSP and 0.22 with FLUSH.

Duration of transition period (drawdown action only)—The transition period represented the amount of time that it would take for the survival rate of juvenile fall chinook to achieve dynamic equilibrium following drawdown. The length of this period depended on assumptions about how long it would take for prey and predator communities to re-establish after drawdown.

Probabilities on alternative hypotheses

Probabilities on alternative hypotheses reflect their relative likelihood or strength of empirical support. PATH did not complete a Weight of Evidence process for fall chinook as we did for spring and summer chinook (Marmorek and Peters 2001), so we simply assumed that all hypotheses were equally likely and conducted sensitivity analyses to determine which of the uncertainties had the greatest effect on outcomes.

Table 3. Definition of alternative assumptions addressed in the analyses.

Model component	Alternative assumptions
Total passage mortality (M) and proportion transported (P_{bt})	CRiSP estimates Fall FLUSH estimates
Relative post-Bonneville survival of transported fish outside of the hydrosystem (D)	D1: retrospective D values estimated from spawner–recruit data using eq. 1 with STEP set = 0 (maximum likelihood estimate of D = 0.05). Prospectively, D increases to 0.24 (mean value estimated from 1995 PIT-tag data), because starting in brood year 1992, smolts were released midchannel rather than along shore (where large concentrations of predators were observed). D2: Retrospective and prospective D values = 1.0 (based on transportation studies of Hanford Reach fall chinook conducted at McNary dam in 1978–1983). D values for Hanford fish may not apply to Snake River fish because of differences in genetics, spatial distribution, smolt size, and outmigration timing. D3: Retrospective and prospective D values estimated from spawner–recruit data using eq. 1. This approach maximized fit of the life-cycle model to spawner–recruit data but assumed that historical estimates were applicable in prospective scenarios despite changes in transportation methods after 1991 (the last year of data used to estimate D). D4: Retrospective and prospective D = 0.2 (mean estimate from 1995 and 1996 PIT-tag data).
Post-Bonneville mortality (STEP)	Hydro: future STEP = value selected from posterior distribution, unless the Snake River dams are breached (action A3), in which case STEP = 0. Assumed that STEP increase in mortality in brood year 1976 was the result of delayed effects of passing through or around the four lower Snake River dams, which were in full operation by that time. Stock viability: future STEP = a value selected from posterior distribution, even if Snake River dams are breached. Assumed that 1976 STEP increase in mortality was the result of factors unrelated to hydrosystem actions or climate (e.g., prevalence of disease) and will persist indefinitely. Regime shift: future STEP alternates according to 30-year cycles in ocean climate. In poor climatic periods (simulation years 1997–2005, 2036–2065, and 2096), STEP selected from its posterior distribution. In good climatic periods (simulation years 2006–2035 and 2066–2095), STEP = 0.0.
Pre-removal period before drawdown	3 years 8 years
Juvenile survival rate after drawdown	Survival rate through drawndown reach = 0.89; average in-river survival rate (including unimpounded reach and four remaining dams and reservoirs) = 0.51 (CRiSP) and 0.39 (FLUSH). Survival rate through drawndown reach = 0.61; average in-river survival rate = 0.35 (CRiSP) and 0.30 (FLUSH).
Transition period after drawdown	2 years: assumed aquatic invertebrates re-establish quickly after major disturbances (e.g., Gore 1979); predators exert little pressure on juvenile salmonids in free-flowing conditions (Ward et al. 1995). 10 years: estimated time required for re-establishment of benthic macroinvertebrate habitat and communities (Pacific Northwest Laboratory 1995) and for stabilization of feeding behaviour and population dynamics of predators.
Ocean and in-river harvest	1. Ocean: Sample from 1985–1996 harvest rates[a] In-river: Current schedule[b] 2. Ocean: Reduced by 15% relative to 1985–1996 In-river: Current schedule 3. Ocean: Reduced by 50% relative to 1985–1993 In-river: Current schedule 4. Ocean: Reduced by 50% relative to 1985–1993 In-river: 50% reduction at lower Snake River run sizes, no increase in harvest rates until escapement exceeds 3750 spawners 5. Reduced by 75% relative to 1985–1993 In-river: Same as scenario 4
Upstream survival rates	Affected by construction and removal of dams Not affected by construction and removal of dams

Note: All assumptions except harvest and upstream survival rates were formally incorporated into the decision analysis; harvest and upstream survival assumptions were explored through sensitivity analyses. Alternative assumptions took the form of different parameter values in the passage or life-cycle models. CRiSP, Columbia River Salmon Passage; FLUSH, Fish Leaving Under Several Hypotheses.

[a] The U.S.–Canada Pacific Salmon Treaty was implemented in 1985.

[b] Based on the 1996–1998 Management Agreement for Upper Columbia River Fall Chinook.

Decision analysis framework

The six uncertainties and their alternative hypotheses resulted in 16 possible outcomes (probabilities of exceeding survival and recovery thresholds) for action A2 (maximize transportation) and 128 possible outcomes for action A3 (natural river drawdown of four Snake River dams). These outcomes provided the basis for identifying key uncertainties and evaluating the performance of actions across uncertainties. To identify which uncertainties had the most influence on outcomes, we applied a Categorical Regression Tree (CART) analysis to the complete set of outcomes for all actions (Breiman et al. 1984; Watters and Deriso 2000). We used box-and-whisker plots of distributions of outcomes to compare the performance of actions across the range of uncertainties.

Sensitivity analyses

We conducted sensitivity analyses to explore how results were affected by assumptions about future harvest management and effects of dams on adult survival rates during upstream migration (Table 3). Alternative harvest strategies incorporated reductions in ocean harvest rates on Snake River fall chinook ranging from 15 to 75% (relative to harvest rates occurring since 1985) in conjunction with both current in-river harvest rates and a hypothetical, conservation-based in-river harvest schedule.

Model runs for the drawdown action (A3) assumed that average upstream adult survival rates would increase from 0.42 to 0.83 following drawdown. We explored an alternative assumption in which upstream survival rates were insensitive to the presence of dams, have remained at current levels (averaging around 0.42) throughout the historical period, and will remain at current levels if drawdown occurs. This assumption required re-estimation of historical recruitment because the original estimates had assumed that upstream survival rates declined when the dams were completed in the early 1970s. Because this assumption changed recruit estimates, it affected results for both the maximize transportation (A2) and the drawdown (A3) action.

Results

Retrospective analysis

We selected the following model structure for prospective modeling:

$$(5)\qquad R_t = (S_{\text{wild}_t} + E \cdot S_{\text{other}_t})\mathrm{e}^{a}\,\mathrm{e}^{-b(S_{\text{wild}_t} + E \cdot S_{\text{other}_t})}\mathrm{e}^{-M_t} \times (DP_{bt} + 1 - P_{bt})\mathrm{e}^{-\text{STEP}}\,\mathrm{e}^{g \cdot e_t(\text{des})}\mathrm{e}^{\varepsilon_t'}$$

where the terms are defined as in eqs. 1 and 2. Selection of model components was based on the relative fits of the 30 alternative models to the spawner–recruit data (as measured by AIC and BIC scores; Table 2) and on the need to allow for implementation of alternative hypotheses about passage- and nonpassage-related factors.

The selected model in eq. 5 had a relatively complex structure that included passage model values for M and P_{bt}. These models had better fits than the simplest two-parameter models but the same or worse fits than models of intermediate complexity (compare models 1, 13, 25, 27, 29, and 30 in Table 2). However, including passage models provided convenient mechanisms for modeling direct effects of hydrosystem actions. We included both CRiSP and FLUSH passage models as alternative hypotheses, although CRiSP estimates provided a better fit than did FLUSH (model 1 vs. model 13). We estimated E from spawner–recruit data to account for an interaction between E and D estimates, although estimating E produced similar (using AIC) or worse (BIC) fits than fixing E at 0.7 or higher (model 1 vs. models 10–12; model 13 vs. models 22–24). E and D were related because hatchery production and the intensity of transportation increased around the same time in the historical period (Table 1). Therefore, a low E (ineffective hatchery spawners) required higher post-Bonneville survival of transported fish (higher D) to produce observed spawner–recruit survival rates. Equation 5 also included a climate factor based on joint Snake River and Deschutes residuals. This approach resulted in a better fit than either ignoring climate effects or using an alternative approach (model 1 vs. models 2 and 5–8; model 13 vs. models 14 and 17–20).

There was an interaction between D and STEP. High mortality of transported fish in the estuary and ocean (implied by low D values obtained when D was estimated from historical spawner–recruit data) explained declining recruitment after transportation began in brood year 1975 and left little mortality to assign to STEP. Consequently, STEP = 0 whenever D was estimated. This suggested that the increase in mortality in the early 1980s (Fig. 2) coincided more closely with the increase in transportation that occurred at that time (Table 1) than with any STEP increase in mortality in 1976 or 1970. Conversely, when D was fixed at a relatively high value (e.g., models 9 and 21), the model estimated a nonzero value for STEP to account for declining recruitment after brood year 1975. This interaction between D and STEP led to two forms of eq. 5 for use in prospective modeling. In the Fall-D model, D was estimated and STEP was set to zero. This form was most consistent with spawner–recruit data and with the hypothesis that the ineffectiveness of transportation best explained observed patterns in survival anomalies. In the Fall-S model, D was a fixed input value and STEP was estimated starting in brood year 1976 (this start year was more consistent with the data than 1970; model 27 vs. model 28). Specifying a fixed input value of D acknowledged that future D values may differ from historical estimates and allowed the model to estimate a measurable STEP for representing the hydro, stock viability, and regime shift explanations for observed patterns in survival.

Finally, PATH explored the effects of individual years of spawner–recruit data. Data from brood year 1991 had a large influence on estimates of D (values were higher if 1991 data were omitted; Hinrichsen 2001). Survival rates were much lower in that year than in other years (Fig. 2), whereas the proportion transported and the proportion of hatchery fish spawning in the Snake River were both high (Table 1). We did not exclude 1991 data from the prospective analyses because there were no anomalous circumstances (e.g., higher measurement error than in other years) to suggest that it should be.

Prospective analysis

Relative effects of uncertainties

The CART analysis showed that the assumed effects of the actions had little influence on probabilities of exceeding the survival threshold of 300 spawners over 24 years. This was largely because the survival improvements assumed to result from drawdown did not take effect until 7–20 years after the start of the simulations. Hypotheses about the effectiveness of transportation (*D* values) and passage survival rates (passage models) accounted for virtually all of the relatively small variance in this metric. CART results were different for the longer-term performance measures (probability of exceeding survival and recovery thresholds of over 100 and 48 years, respectively). There, differences in assumptions associated with the transportation and drawdown actions (such as the assumed increase in juvenile and adult survival rates associated with drawdown) were the most important influence in determining model results. *D* hypotheses had the next largest effect on the long-term measures, followed by hypotheses about post-Bonneville mortality (STEP). The combined effects of the actions and these hypotheses accounted for virtually all of the variance in the 100-year survival and 48-year recovery metrics.

Performance of actions across uncertainties

Actions A2 (maximize transportation) and A3 (natural river drawdown of four Snake River dams) produced similar distributions of probabilities of exceeding the survival threshold of 300 spawners (Fig. 5). Means and medians of the distributions were generally slightly higher for A3 but greater than 0.9 for both actions. The high probabilities of exceeding the survival escapement threshold were not surprising given that the average abundance of natural spawners from 1993 to 1997 (411 fish; Table 1) exceeded the threshold.

Exceeding the recovery threshold of 2500 spawners proved to be much more difficult to achieve. This threshold was similar to the average escapement over the complete time series, which included some years with high escapements (Table 1). The distribution of probabilities of exceeding this threshold over 48 years for A2 (maximize transportation) was broad with a mean of 0.53 and a median of 0.56. With A3 (drawdown), however, the distribution was highly skewed and around 80% of the 128 combinations of assumptions projected that the recovery threshold would be exceeded with a probability of 1. The mean and median of the distribution were both close to 1 with action A3.

The overall ranking of the transportation (A2) and drawdown (A3) actions, based on probabilities of exceeding recovery thresholds, was unaffected by the *D* hypotheses (Table 4). Probabilities for A3 were higher than those of A2 with all *D* hypotheses, although the difference was smaller when *D* was assumed to either improve over time (as in hypothesis D1, which assumed a threefold improvement in prospective *D* values over the retrospective value) or remain high and constant (as in hypothesis D2, where $D = 1.0$). Further sensitivity analysis showed that for A2 and A3 to produce similar outcomes, *D* must either improve by 3.5-fold over retrospective values or remain constant at 1.8 or higher.

Sensitivity analyses

In general, alternative assumptions about harvest and upstream survival rates did not affect the overall ranking of actions (Table 4). With hypotheses D1 and D2 and the most extreme reductions in ocean and in-river harvest rates (scenarios 4 and 5), the increases in probabilities for A2 were large enough to approach base results (i.e., with no change in harvest rates) for the drawdown action A3. However, with hypotheses D3 and D4, base A3 results still exceeded those of A2, regardless of the assumed reductions in harvest rates.

Fig. 5. Distributions of probabilities of exceeding (*a*) the survival threshold (300 spawners) over 24 years, (*b*) the survival threshold over 100 years, and (*c*) the recovery threshold (2500 spawners) over 48 years for the two hydrosystem actions. There were 16 outcomes for the transportation action and 128 for the drawdown action. Distributions of 24-year and 100-year survival metrics were similar for the two actions, but drawdown produced higher and less variable probabilities of exceeding the recovery escapement threshold than did maximizing transportation.

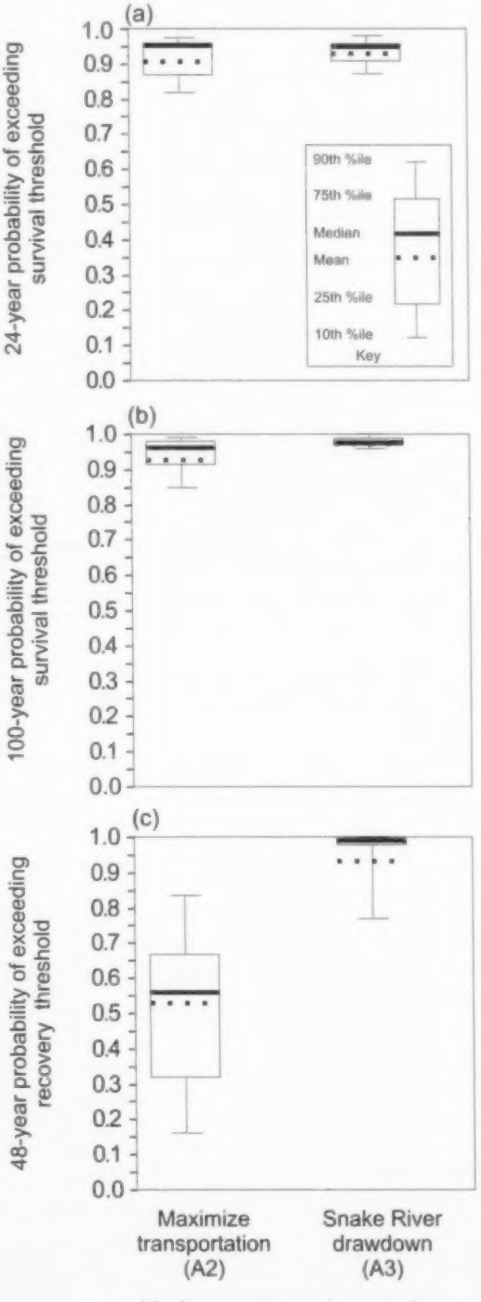


Table 4. Probabilities of exceeding the recovery threshold over 48 years under different *D*, harvest, and upstream survival assumptions.

	Base assumptions[a]		Harvest scenarios (A2 results)				Alternative upstream survival rate under drawdown[b]	
D hypothesis	A2	A3	2	3	4	5	A2	A3
D1	0.87	1.00	0.89	0.95	0.97	0.97	0.92	1.00
D2	0.68	0.83	0.70	0.76	0.81	0.83	0.42	0.39
D3	0.28	1.00	0.31	0.38	0.44	0.47	0.17	1.00
D4	0.34	1.00	0.37	0.48	0.56	0.61	0.22	0.91

Note: Harvest scenarios and *D* hypotheses are defined in Table 3. Results for all *D* hypotheses are averaged over passage model and (for drawdown only) pre-removal, juvenile survival rate, and transition period hypotheses. Results for D2 and D4 are also averaged over the three post-Bonneville mortality (STEP) hypotheses. Only results for the maximize transportation action (A2) are shown for the harvest scenarios because results for the drawdown action (A3) under current harvest conditions were already high, leaving little room for improvement by reducing harvest rates. Results for action A3 were higher than A2 under most sets of assumptions.

[a] Results in these columns assume harvest scenario 1 from Table 3 and that upstream survival rates declined when Snake River dams were completed in the early 1970s and will improve if the drawdown action (A3) is implemented.

[b] The alternative assumption was that upstream survival rates were unaffected by dams, have remained at current levels throughout the entire historical period, and will remain at current levels if the drawdown action (A3) is implemented.

Assuming that upstream survival rates were unaffected by dams generally resulted in reduced probabilities of exceeding recovery thresholds for both the transportation (A2) and drawdown (A3) actions (Table 4). The effect of this alternative assumption on relative outcomes for the two hydrosystem actions depended on the *D* assumption. With D1 and D2, the alternative upstream survival rate assumption resulted in recovery probabilities for A2 that approached or exceeded those of A3. With low *D* values (D3 and D4), probabilities of exceeding the recovery threshold for A3 were still higher than those of A2.

Discussion

The paucity of important spawner–recruit, juvenile survival, and transportation data resulted in a simpler life-cycle model, a much simpler decision tree, and a smaller number of possible outcomes of actions for fall chinook (16 for maximize transportation and 128 for drawdown, compared with 240 and 1920, respectively, for spring–summer chinook). We found that decision analysis was just as important in this data-poor situation as it was in the data-rich spring–summer chinook analysis because it helped us to focus analyses of limited data on testing specific hypotheses that underlie alternative decisions, rather than hypotheses that were ultimately less relevant to decision making. Moreover, the sensitivity analyses conducted as part of the decision analysis were useful for identifying key information gaps and prioritizing future research and potential adaptive management experiments.

The most significant consequence of the lack of information for fall chinook was that we were unable to draw firm conclusions about the long-term effectiveness of transportation. Although our results for the transportation action (as measured by the probability of exceeding the recovery threshold) were generally worse than results for drawdown, the difference in performance between the two actions was highly dependent on assumptions about the relative survival rate of transported fish once they are released from the truck or barge (i.e., the value of *D*), future harvest rates, and the effects of dams on upstream survival rates.

Decision makers may find these results unsatisfying because they do not provide unambiguous policy direction. However, they have at least two useful implications. First, they clarify what decision makers must assume about the relative likelihood of alternative *D* hypotheses, the improvement in upstream survival rates following drawdown, and the feasibility of implementing dramatic changes to ocean and in-river harvest schedules to justify a particular course of action. Second, the results demonstrate the relative biological risk associated with the two actions. Both the maximize transportation and drawdown actions produced high probabilities of exceeding the survival threshold of 300 spawners, although this was not a particularly difficult objective to meet. However, the drawdown action resulted in higher probabilities of exceeding the recovery threshold (2500 spawners) than did the transportation action over a wide range of uncertainties and assumptions. Therefore, if a hydrosystem decision must be made now, the most biologically risk-averse action would be to implement drawdown because it was projected to produce favorable outcomes over the widest range of uncertainties and assumptions.

The existence of uncertainty is often used to justify delaying a decision and maintaining the status quo because of the perceived risk of acting when a favorable outcome cannot be guaranteed (Peterman and Anderson 1999). Our results show that the maximize transportation action (which is most similar to status quo operation of the hydropower system) incurs significant risk of not achieving long-term recovery goals. However, if a decision must be delayed, we suggest that the interim focus should be on reducing uncertainty in *D* values using transportation studies. These may be more feasible in the near future as supplementation with hatchery-raised fish increases the number of fall chinook spawners returning to the Snake River. Future transport studies will not provide useful data on historical *D* values, but they could be used to narrow the plausible range of prospective *D* values and eliminate extreme hypotheses such as D3 ($D = 0.05$) and D2 ($D = 1.0$). Once a plausible range of prospective *D* values was identified, one could perform sensitivity analyses of prospective:retrospective *D* ratios to see what the retrospective *D* would have to have been for escapement under the transportation action to exceed the recovery threshold. Then, those retrospective *D* values can be compared with available information such as spawner–recruit data to see if the implied historical effectiveness of transportation is consistent with historical patterns in overall survival rates.

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Zebra mussels (*Dreissena polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: system-wide effects and behavioural mechanisms

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Abstract: The aggregate impact of an exotic species introduction, such as the zebra mussel (*Dreissena polymorpha*), may involve a large number of biotic and abiotic interactions within the recipient ecosystem. We used laboratory experiments and field data to assess effects of zebra mussels on both foraging success of yellow perch (*Perca flavescens*) and activity of the amphipod *Gammarus fasciatus*. In two laboratory experiments zebra mussel clusters reduced the rate at which yellow perch captured amphipods. Yellow perch captured fewer amphipods when zebra mussels were present at two light levels (<2.1 and >214 lx) and across a range of prey densities (76–1500 amphipods·m^{-2}). The effect of zebra mussels on amphipod activity depended on light level. Yellow perch captured fewer amphipods in the presence of mussel clusters than when plants were present. The frequency of amphipods in the diets of adult yellow perch in Oneida Lake increased after zebra mussel introduction, but the increase was greater in low mussel density habitats. Our laboratory results and field observations suggest that zebra mussels affect yellow perch foraging on amphipods through increased structural complexity (negative) and increased light penetration (positive), but not through increased prey density.

Résumé : L'impact global de l'introduction d'une espèce exotique, telle que la Moule zébrée (*Dreissena polymorpha*), peut affecter de nombreuses interactions biotiques et abiotiques dans l'écosystème qui la subit. Des expériences en laboratoire et des données de terrain ont servi à déterminer les effets des Moules zébrées à la fois sur le succès de la quête de nourriture chez la Perchaude (*Perca flavescens*) et sur l'activité de l'amphipode *Gammarus fasciatus*. Dans deux expériences de laboratoire, la présence de grappes de Moules zébrées a réduit le taux de capture d'amphipodes chez la Perchaude. Les Perchaudes attrapaient moins d'amphipodes en présence des Moules zébrées à deux intensités lumineuses (<2,1 et >214 lx) sur une gamme de densités de proies, de 76 à 1500 amphipodes·m^{-2}. L'effet des Moules zébrées sur les amphipodes dépendait de l'intensité lumineuse. Les Perchaudes capturaient moins d'amphipodes en présence de grappes de moules qu'en présence de plantes aquatiques. La fréquence des amphipodes dans le régime alimentaire des Perchaudes au lac Oneida a augmenté après l'introduction des Moules zébrées, mais cette hausse a été plus importante dans les habitats où les moules avaient une densité faible. Nos résultats en laboratoire et nos observations sur le terrain laissent croire que les Moules zébrées affectent la consommation des amphipodes par les Perchaudes, de façon négative en augmentant la complexité structurale du milieu et de façon positive en favorisant la pénétration de la lumière; la densité des proies ne s'est cependant pas accrue.

[Traduit par la Rédaction]

Introduction

Species introductions are one of the most significant environmental problems currently facing freshwater ecosystems (Richter et al. 1997). The ultimate effects of a species introduction are difficult to predict, partly because of complex organism–organism and organism–habitat interactions that occur in all ecosystems. For example, an introduced species may negatively affect competitors and thereby have an indirect negative effect on species at higher trophic levels that consume the native competitors. Even when pairwise interactions between species are understood, the complex interactions are difficult to predict (Peckarsky and McIntosh 1998). Further, some organisms can alter habitat (ecosystem engineer sensu Jones et al. 1994) and thereby increase the number of their indirect interactions with other species. An example of an introduced species that may have complex, system-wide effects on freshwater ecosystems that are diffi-

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cult to predict is the zebra mussel (*Dreissena polymorpha*), which was introduced to the Laurentian Great Lakes in 1986 (Herbert et al. 1989). These mollusks are associated with multiple system level changes, including increased water clarity (Fahnenstiel et al. 1995; Mayer et al. 2000), increased macrophyte growth (Skubinna et al. 1995), and increased densities of benthic invertebrates near mussel clusters (e.g., Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998). However, the way in which these alterations affect higher trophic levels, such as fish, is not clear.

Increases in water clarity and light penetration may affect visually feeding fish, especially those that feed on or near the bottom, by (*i*) increasing foraging success, (*ii*) increasing the time when light is sufficient for foraging, and (*iii*) increasing the bottom area with sufficient light for foraging. However, increased light penetration may alter benthic invertebrate behaviour in a manner that reduces their vulnerability to fish predation. In mobile freshwater invertebrates such as amphipods, activity has been reported to decrease during the day or with increased light for several species (Wallace et al. 1975; Holomuzki and Hoyle 1990). Prey activity level may influence fish foraging success (Cooper and Crowder 1982); therefore, a reduction in activity level of mobile prey items may offset gains in foraging success owing to increased visual acuity associated with light penetration. The net effect of increased light penetration on fish foraging success will depend on the combined effects on predator and prey.

Multiple studies have attributed the primary effect of zebra mussels on local densities of benthic invertebrates to the effect of increased structural complexity (Ricciardi et al. 1997; Stewart et al. 1998). The foraging success of many benthivorous fish is reduced in structurally complex habitats, e.g., artificial substrates (Russo 1987), leaf litter (Holomuzki and Hoyle 1990), macrophytes (Nelson 1979), and macroalgae (Drake et al. 1995). Although, González and Downing (1999) found that mussel clusters reduced only the foraging rate of bluegill (*Lepomis macrochirus*) and not of yellow perch (*Perca flavescens*). One reason that fish may forage less successfully in structurally complex habitats is that some mobile invertebrates like amphipods decrease activity with increased substrate complexity (Holomuzki and Hoyle 1990). In addition to the possible effects of zebra mussel clusters themselves, an increase in the extent or density of rooted macrophytes may also increase structural complexity and reduce the foraging efficiency of fish over an even larger portion of a lake's bottom.

It is also necessary to consider the spatial extent of each direct and indirect interaction. An increase in light penetration is potentially a system-wide effect; lake morphometry will determine the depth to which this effect may be important. The effect of increased structural complexity caused by mussel clusters or macrophytes will be localized, though the area affected by each will differ with lake morphometry and substrate type. In most systems zebra mussels can only colonize hard substrates like rock or clam shells, though in Lake Erie *Dreissena* are now reported to colonize soft substrates (Berkman et al. 1998). Therefore, the number, strength, and spatial extent of biotic and abiotic interactions will determine the impact of an introduced species.

It is not surprising then that there is no consensus as to how zebra mussel introduction affects fish populations in natural systems. Growth of young-of-the-year (YOY) yellow perch and white perch (*Morone americana*) in Lake Erie showed no clear trend in association with zebra mussel introduction (Graham 1993). The only long-term study to address the effect of zebra mussel introduction on fish has been in Oneida Lake, N.Y., where growth of YOY yellow perch increased. However, adult yellow perch growth did not change even though the proportion of the population that consumed both planktonic and benthic invertebrates increased, probably owing to increased water clarity associated with zebra mussel grazing (Mayer et al. 2000).

In this study, we use laboratory experiments to test the effects of light level and zebra mussel presence on the behaviour of yellow perch and the amphipod *Gammarus fasciatus*. We also test the effect of *G. fasciatus* density on yellow perch foraging success in the presence of zebra mussels, macrophytes, and bare lake sediment. We then use the results of these laboratory studies to interpret long-term field data on the percent frequency of occurrence of amphipods in the diet of yellow perch from Oneida Lake, N.Y. Oneida Lake is eutrophic, shallow, and well mixed, with a surface area of 206.7 km^2 (Mills et al. 1978). Zebra mussels were first observed in 1991 and have since colonized most areas that provide hard substrate. Combining laboratory experiments, which elucidate species interactions, and long-term field data, which integrates a large number of food-web and abiotic interactions, is important for understanding the effects of species introductions to ecosystems.

Methods

Laboratory experiments

Age-1 yellow perch, zebra mussels, and amphipods were collected from Oneida Lake in the summers of 1996 and 1997. Yellow perch were seined and caught in wire traps, transferred to 800-L stock tanks, maintained on a photoperiod of 14 h light : 10 h dark, and fed commercial food pellets daily between 1200 and 1700 hours. SCUBA divers collected zebra mussel clusters attached to the shells of dead unionid clams; these were stored in aquaria and fed powdered algae frozen in ice cubes to allow for slow release of algal particles. Amphipods were collected with dip nets and from zebra mussel clusters. They were kept in buckets for at least 20 h and were fed senesced leaves and other plant matter. Amphipods were not size-sorted for experiments, but were haphazardly chosen from the available size range.

All yellow perch and amphipods were acclimated in experimental containers overnight; fish were isolated in plastic holding chambers (120 mm × 120 mm × 340 mm) with 1-mm mesh. Trials occurred between 1100 and 1400 hours. Amphipods used in experiments with fish were not used again, as the fish may have selected the more active individuals. Air stones were removed from the experimental containers 30 min before the beginning of each experiment to prevent amphipods from clinging to them. At the end of each trial fish were euthanized with tricaine methanesulfonate. Fish total length was recorded, and stomach contents were examined to determine the number of amphipods captured.

Light and zebra mussels

Two sides and the bottom of 29-L aquaria were covered with black plastic to maintain a constant background over as much of the surface area as possible. Each trial was filmed using an infrared-sensitive video camera; aquaria were lighted from above with two incandescent bulbs on a dimmer switch. A lamp with an infrared filter was used to illuminate the experimental aquaria from behind for the dark and low light treatments to allow filming.

Experimental treatment combinations consisted of amphipods with and without zebra mussels and with and without yellow perch at three light intensities in a full-factorial design. Five sequential blocks of experiments consisted of the 12 treatment combinations in a randomly determined order, and three trials were performed each day. Fish-holding chambers were also added to the non-fish treatments to include the effect that this disturbance may have had. The number of amphipods used (40) was approximately the average density on soft substrates in Oneida Lake from 1975 to 1995 ($294 \cdot m^{-2}$, unpublished data, Cornell Biological Field Station, 900 Shackelton Point Road, Bridgeport, NY 13030, U.S.A.). In the zebra mussel treatment, nine unionid half-shells encrusted with zebra mussels covered approximately 25% of the bottom of each aquarium.

Three light conditions, dark (0 lx), low light (0.9–2.2 lx), and high light (214–252 lx), represent a range of light intensities shown to impact the visual acuity and reaction distances of fish (Confer et al. 1978; Vinyard and O'Brian 1976; Mills et al. 1986). Light intensities were measured at several locations within each aquarium using a Protomatic light meter (7868 2nd St., Box 21, Dexter, MI 48130, U.S.A.) and an average value was calculated. The infrared light did not appear to affect amphipod activity, and Westin and Aneer (1987) successfully used infrared light in marine amphipod activity experiments.

Each trial lasted 20 min. Amphipod activity was measured as the number of ascents made above a horizontal line 54 mm above the aquarium bottom. Most amphipods ascended above this line when leaving direct contact with the bottom. Amphipods in amplexus (or precopula) were counted as one because they could not always be distinguished as separate individuals. Fish feeding attempts were categorized and quantified from the videotapes as attacks when a rapid abrupt movement toward a prey item occurred.

Amphipod ascents, perch attacks, and captures were square-root transformed for analysis to increase normality and to stabilize variance. Amphipod ascents were analyzed to detect significant effects of light intensity, the presence of zebra mussel clusters, and the presence of fish using a three-factor analysis of variance (ANOVA). Yellow perch attacks and captures were analyzed to detect effects of light intensity level, the presence of zebra mussel clusters, and experimental block using a multifactor multivariate ANOVA (MANOVA). The effect of experimental block ($N = 1–5$) was initially tested to detect temporal variation during the experimental period; when not significant, it was removed from the analysis. If MANOVAs were significant, we conducted individual two-factor ANOVAs to test the effects of light and mussel clusters on the mean number of attacks and captures. When interaction terms were significant, the simple effects, i.e., the differences among levels of one factor within levels of the other factors, were examined using pairwise contrasts with α adjusted for the number of pairwise comparisons ($0.05/9 = 0.0056$). Correlation analysis was also used to assess relationships between amphipod ascents and yellow perch attacks and captures as the perch were expected to feed more with increased amphipod activity. Correlations between yellow perch total length and foraging measures were also considered, because we expected that larger fish might forage more successfully.

Amphipod density and substrate

Experiments to test the effect of amphipod density on number of captures by age-1 yellow perch with different substrates were conducted in three identical 0.92-m diameter plastic wading pools. The substrate treatments included (*i*) 1–2 cm of lake sand evenly spread across the pool's bottom, (*ii*) a layer of sand and 21 evenly spaced zebra mussel clusters, and (*iii*) a layer of sand and 21 evenly spaced clusters of *Elodia* spp. stems attached to small stones. The three pools were placed directly under a bank of fluorescent lights, which were turned on in the morning of each experiment.

Amphipod densities tested were 76, 152, 228, 304, 380, 456, 532, 608, 684, 760, 912, and $1521 \cdot m^{-2}$. Each density was tested in each substrate type and densities 152 and 304 were replicated ($N = 42$). These amphipod densities span the range seen on soft substrates in Oneida Lake. At the beginning of each trial, fish were released from the containment box, and allowed to feed for one hour. These trials were not filmed. The number of amphipods consumed was determined by examining the stomach contents of each fish.

Predators may respond to an increase in prey density with a type II or asymptotic functional response (Holling 1959). We chose to transform the number of amphipods consumed ($\log_{10}(x + 1)$) to linearize the relationship so we could include this analysis in a general linear model. The number of amphipods consumed was compared among substrate types and across densities using analysis of covariance (ANCOVA) with amphipod density as the covariate. We included an interaction term to test for differences among the slopes of the amphipod density – amphipods consumed relationship across the different substrate types. A nonsignificant interaction term was removed from the model and analysis was rerun. Pairwise contrasts were used to test for differences between the three habitat types; α was adjusted for the number of pairwise comparisons ($0.05/3 = 0.017$). Additionally, correlation analysis was used to test the relationship between total fish length and number of amphipods consumed to determine if this was a significant source of variance.

Yellow perch field diet data

We compared the number of adult yellow perch caught and the proportion of the population that consumed amphipods in a high-density and low-density zebra mussel habitat before and after zebra mussel introduction in Oneida Lake. We further compared the proportion of the population that consumed amphipodswith an index of light penetration andwith an index of amphipod density. The yellow perch population of Oneida Lake has been monitored since 1987 using weekly gillnet sets from June until mid-September. Variable mesh, multifilament gillnets (38- to 101-mm stretch mesh) were set on bottom at the same 15 locations sequentially from June to September, i.e., a net was set at site A in the first week of every sampling season, at site B in the second, and so on. Nets were set at sunset and retrieved at 0730 hours. Fish were counted, the stomach contents of yellow perch were examined each week, and the number of perch containing amphipods was noted. If more than 60 yellow perch were caught in a week, a subsample of 50–60 fish was selected for stomach content analysis. For diet analysis we included only the occasions (year and site) when more than six fish were examined and we excluded any sites for which less than two years in both the pre- and post-zebra mussel time period were available. The number of yellow perch caught was not transformed for analysis, but the proportion with amphipods in their diet was arcsine square-root transformed for all statistical comparisons (Zar 1984).

Each site was classified as proximal to a shoal (high zebra mussel density) or as open (low zebra mussel density). The substrate at shoal sites was composed of a mosaic of various sized cobble and some softer substrates, whereas substrate at open sites was soft, ranging from organic mud to clay. In 1997 zebra mussel density in Oneida Lake was $45\,000 \cdot m^{-2} \pm 21\,000$ (95% confidence interval, CI) on hard substrates such as cobble and $3000 \cdot m^{-2} \pm 2800$ 95% CI on soft substrate (Idrisi et al. 2001). We compared the number of yellow perch caught and the proportion of the population that consumed amphipods in shoal and open habitats, and in the pre- and post-zebra mussel periods using two-factor ANOVAs (habitat and time period).

Secchi depth (an index of light penetration) significantly increased after zebra mussel introduction to Oneida Lake (Mayer et al. 2000). Secchi depth was measured usually weekly, using a 22-cm diameter black and white disc, normally at five open-water stations from June to September of 1987 to 1999. The five station values were averaged to provide weekly means, which were averaged to provide monthly means. Each gillnet event was matched to the closest average weekly Secchi depth. In the few cases when a weekly Secchi depth was not available, we substituted the monthly value. Samples of benthic invertebrates were collected approximately biweekly at three stations in Oneida Lake with an Ekman grab from 1987 to 1998. Sites included two deep sites (>11 m) and one shallow site (≈3.5 m). All sites had a soft mud bottom. Contents of each grab were passed through a 253-μm mesh screen and preserved in 70% alcohol and Rose Bengal. Monthly mean density of amphipods was calculated as an index of amphipod availability and these values were $\log_{10}(x + 1)$ transformed for statistical analysis to increase normality and to stabilize variance. We used multiple regression to develop relationships between the proportion of the yellow perch population that consumed amphipods and Secchi depth and the density of amphipods.

Results

Laboratory experiments

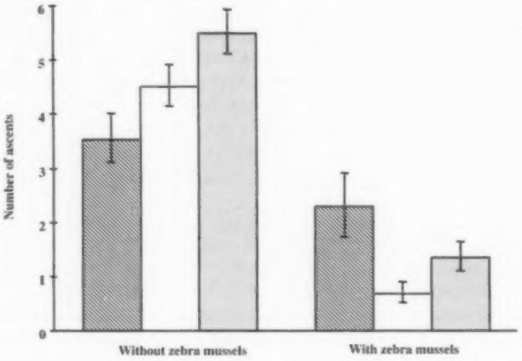
Light and zebra mussels

Experimental block, which was initially included as a factor in our analysis to determine if there were temporal changes in amphipod activity or perch foraging success, did not have a significant effect on amphipod or fish behaviour ($P > 0.05$) and was excluded from all further analyses.

The presence of zebra mussel clusters and the interaction between zebra mussel presence and light intensity (Fig. 1; Table 1) significantly affected amphipod activity. The presence of zebra mussel clusters consistently lowered amphipod activity, regardless of light level (Fig. 1; Table 1). However, the direction of the effect of light intensity on amphipod activity changed depending on the presence or absence of zebra mussels. In the absence of zebra mussels, amphipods increased activity as light intensity increased. In contrast, in the presence of zebra mussels amphipods were more active in darkness than at either light level, though not significantly so (Table 1).

MANOVA indicated that light (Wilk's $\Lambda = 0.6537$, $P = 0.0407$), zebra mussel clusters (Wilk's $\Lambda = 0.3988$, $P = 0.0001$), and an interaction of these factors (Wilk's $\Lambda = 0.6421$, $P = 0.0341$) affected the feeding of yellow perch. The univariate ANOVAs showed that zebra mussels significantly affected the number of attacks and that there was a significant interaction between light and zebra mussels. The presence of zebra mussels did not affect the number of attacks by yellow perch on amphipods in total darkness, but did have an effect at the two higher light levels tested (Fig. 2*a*; Table 2). The presence of zebra mussel clusters, light intensity, and the interaction of the two factors significantly affected the number of captures made by yellow perch (Fig. 2*b*; Table 3). When zebra mussels were absent, yellow perch made significantly more captures in the low light than in darkness, although the difference between numbers of captures in darkness and in high light fell short of statistical significance (Fig. 2*b*; Table 3). In the presence of zebra mussels, light had no effect on the number of attacks or captures.

Fig. 1. Activity of the amphipod *Gammarus fasciatus*, indexed by mean (±1 standard error) number of ascents above a line 54 mm above aquarium bottom in 20-min laboratory experiments at three light levels and with and without zebra mussels. Data were transformed for statistical analysis. Hatched bars, 0 lx; open bars, <2.1 lx; shaded bars, >214 lx.



Yellow perch attacks and captures were positively correlated with amphipod activity. Increased amphipod ascents were associated with increased yellow perch attacks ($R = 0.54$, $P = 0.0021$) and captures ($R = 0.70$, $P = 0.0001$). Yellow perch total lengths varied between 81 and 117 mm, but were not significantly correlated to the number of yellow perch attacks or captures.

Amphipod density and substrate

The initial ANCOVA showed that the interaction term between substrate type (categorical variable) and amphipod density (covariate) was not significant ($P < 0.600$); therefore, the interaction term was removed from the model. The overall ANCOVA was significant ($F_{2,41} = 3.107$, $P < 0.038$). The effect of density was not significant (Fig. 3; $F = 0.282$, $P < 0.600$), but the effect of substrate type was significant (Fig. 3; $F = 4.519$, $P < 0.017$). Contrast statements showed that the number of amphipods consumed when mussels were present was lower than the number consumed over sand alone ($P < 0.008$), but not from the number consumed in the presence of plants ($P < 0.700$). The number consumed in the presence of plants was lower than that consumed over sand alone, but did not meet our significance criteria ($P < 0.022$).

The total length of fish used in experiments ranged from 65 to 126 mm, but there was no significant correlation between length and the number of amphipods consumed ($R = -0.14$, $P < 0.36$).

Yellow perch field diet data

The original two-factor ANOVA testing the number of fish caught showed no significant interaction between habitat (shoal and open) and time period (pre- and post-zebra mussel); therefore, the interaction term was removed. The new ANOVA was significant ($F_{2,194} = 4.99$, $P < 0.007$). A larger number of the adult yellow perch were caught at open than were caught at shoal sites (Fig. 4*a*; $F = 7.09$, $P < 0.008$), but there was no difference between the pre- and post-zebra mussel periods (Fig. 4*a*; $F = 2.88$, $P < 0.091$).

Table 1. Analysis of the activity level of the amphipod *Gammarus fasciatus* in laboratory experiments with and without yellow perch and zebra mussels at three light levels (0, 0.9–2.2, and 214–252 lx).

(A) Full model.

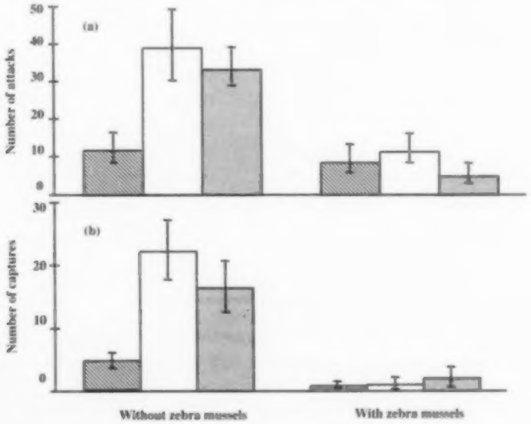
Source	df	SS	*F*	*P*
Light	2	9.33	2.68	0.0785
Zebra mussels	1	133.39	76.69	0.0001*
Yellow perch	1	0.70	0.40	0.5287
Light × zebra mussels	2	23.03	6.62	0.0029*
Light × yellow perch	2	6.76	1.95	0.1541
Zebra mussels × yellow perch	1	2.50	1.44	0.2363
Light × zebra mussels × yellow perch	2	1.58	0.46	0.6366
Error	48	83.48		

(B) Contrasts.

Source	df	SS	*F*	*P*
Mussels vs. without mussels in dark	1	7.56	4.30	0.0429
Mussels vs. without mussels in low light	1	73.16	41.57	0.0001*
Mussels vs. without mussels in high light	1	75.69	43.01	0.0001*
Dark vs. low light, without mussels	1	4.74	2.71	0.1115
Dark vs. high light, without mussels	1	19.16	10.92	0.0027*
Low vs. high light, without mussels	1	4.83	2.75	0.1086
Dark vs. low light, with mussels	1	13.13	7.44	0.0111
Dark vs. high light, with mussels	1	2.47	1.40	0.2470
Low vs. high light, with mussels	1	4.20	2.38	0.1342

Note: $N = 5$ for each treatment combination. Data were square-root transformed for analysis. α was corrected for the number of pairwise comparisons (0.05/9). df, degrees of freedom; SS, sum of squares; *Statistically significant results.

Fig. 2. Mean (±1 standard error) number of attacks and captures of age-1 yellow perch feeding on amphipod prey in 20-min laboratory experiments at three light levels, with and without zebra mussels. Data were transformed for statistical analysis. Hatched bars, 0 lx; open bars, <2.1 lx; shaded bars, >214 lx.



The original two-factor ANOVA testing the proportion of yellow perch that consumed amphipods showed no significant interaction between habitat and zebra mussel time period; therefore, the interaction term was removed. The new ANOVA was significant ($F_{2,157} = 11.83$, $P < 0.001$). A significantly higher proportion of the adult yellow perch sampled consumed amphipods at open than at shoal sites (Fig. 4*b*; $F = 13.31$, $P < 0.001$) and more fish consumed amphipods after zebra mussel introduction than before (Fig. 4*b*; $F = 10.35$, $P < 0.002$). The magnitude of the increase in the proportion of the yellow perch population consuming amphipods after zebra mussel introduction was larger at the open sites compared to the shoal sites (Fig. 4*b*).

At the open sites, the overall multiple regression explaining the proportion of yellow perch that consumed amphipods was marginally significant and very little variation was explained by the model ($P < 0.052$; adjusted $R^2 = 0.07$), the effect of Secchi depth was positive and significant ($P < 0.016$), but the effect of amphipod density was not significant (Fig. 5*a*; $P < 0.706$). Similarly, at shoal sites the overall multiple regression explaining the proportion of yellow perch that consumed amphipods was significant, though very little variation was explained by the model ($P < 0.014$; adjusted $R^2 = 0.07$), the effect of Secchi depth was positive and significant ($P < 0.004$) but the effect of amphipod density was not significant (Fig. 5*b*; $P < 0.395$).

Discussion

Interactions between pairs of species are embedded in complex, multispecies food webs. Ecological theory suggests that behaviourally mediated effects of a perturbation can produce a highly diffuse response (Yodzis 2000). If an introduced species modifies habitat in the sense of Jones et al. (1994, "ecosystem engineer"), we may expect the system response to the perturbation to be especially great because of increased potential for indirect effects on other species. The zebra mussel is a species introduced to North America that modifies habitat as well as having numerous biotic interactions. Zebra mussels may affect light penetration, bottom structural complexity, and invertebrate density. A series of laboratory

Table 2. Analysis of number of yellow perch attacks on the amphipod *Gammarus fasciatus* in laboratory experiments with and without zebra mussels at three light levels (0, 0.9–2.2, and 214–252 lx).

(A) Full model.

Source	df	SS	*F*	*P*
Light	2	12.57	2.97	0.0703
Zebra mussels	1	45.79	21.64	0.0001*
Light × zebra mussels	2	14.75	3.49	0.0468*
Error	24	50.79		

(B) Contrasts.

Source	df	SS	*F*	*P*
Mussels vs. without mussels in dark	1	0.86	0.41	0.5291
Mussels vs. without mussels in low light	1	20.63	9.75	0.0046*
Mussels vs. without mussels in high light	1	39.05	18.45	0.0002*
Dark vs. low light, without mussels	1	18.06	8.71	0.0121
Dark vs. high light, without mussels	1	14.78	6.92	0.0219
Low vs. high light, without mussels	1	0.21	0.10	0.7545
Dark vs. low light, with mussels	1	0.48	0.23	0.6376
Dark vs. high light, with mussels	1	2.17	1.04	0.3285
Low vs. high light, with mussels	1	4.72	2.26	0.1590

Note: $N = 5$ for each treatment combination. Data were square-root transformed for analysis. α was corrected for the number of pairwise comparisons (0.05/9). df, degrees of freedom; SS, sum of squares; *Statistically significant results.

Table 3. Analysis of number of yellow perch captures of the amphipod *Gammarus fasciatus* in laboratory experiments with and without zebra mussels at three light levels (0, 0.9–2.2, and 214–252 lx).

(A) Full model.

Source	df	SS	*F*	*P*
Light	2	8.62	3.75	0.0383*
Zebra mussels	1	62.47	21.64	0.0001*
Light × zebra mussels	2	8.60	3.49	0.0468*
Error	24	107		

(B) Contrasts.

Source	df	SS	*F*	*P*
Mussels vs. without mussels in dark	1	5.50	4.79	0.386
Mussels vs. without mussels in low light	1	41.67	36.27	0.0001*
Mussels vs. without mussels in high light	1	23.90	20.80	0.0001*
Dark vs. low light, without mussels	1	15.38	12.49	0.0041
Dark vs. high light, without mussels	1	8.94	7.26	0.0195
Low vs. high light, without mussels	1	0.87	0.71	0.4175
Dark vs. low light, with mussels	1	0.04	0.03	0.8591
Dark vs. high light, with mussels	1	0.20	0.19	0.6727
Low vs. high light, with mussels	1	0.40	0.38	0.5504

Note: $N = 5$ for each treatment combination. Data were square-root transformed for analysis. α was corrected for the number of pairwise comparisons (0.05/9). df, degrees of freedom; SS, sum of squares; *Statistically significant results.

experiments and long-term field data investigating the potential multiple effects of zebra mussels on yellow perch foraging suggested that there is a strong positive effect of increased light penetration, a weaker negative effect of structural complexity, and virtually no effect of increased prey density. Controlled experiments are vital to understanding the mechanisms behind species interactions, but long-term field data are required to understand the whole-system effect of a species introduction, which integrates direct and indirect effects involving both other species and habitat.

Our laboratory experiments showed that zebra mussel clusters reduced the yellow perch capture rate of amphipods at two light levels, and across a range of prey densities. These experiments suggested that the local negative effect of mussel habitat complexity will outweigh the positive effects of increased light penetration or prey density in systems where zebra mussels are introduced. Field data from Oneida Lake showed that yellow perch did not shift the habitat in which they feed to avoid the high-density mussel areas in the way that bluegill maximize foraging return by moving from vegetated to open-water habitats (Mittelbach 1981). In the lake, yellow perch in both low and high mussel density

Fig. 3. Number of amphipod prey captured by yellow perch as a function of prey density with (*a*) zebra mussels, (*b*) rooted plants, or (*c*) bare sand bottoms in 1-h laboratory experiments. Data were $\log_{10}(x+1)$-transformed for statistical analysis and display. Lines are linear regressions, fitted to data from each habitat type.

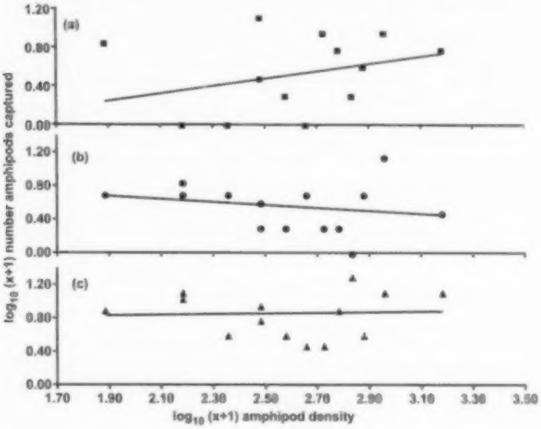


Fig. 4. Mean (±1 standard error) percent of the adult yellow perch (*a*) that consumed amphipods and (*b*) number caught in gillnets at two habitat types in Oneida Lake from June to September during pre-zebra mussel (1987–1991) and post-zebra mussel (1992–1999) periods. Proportion data were arcsine square-root transformed for statistical analysis.

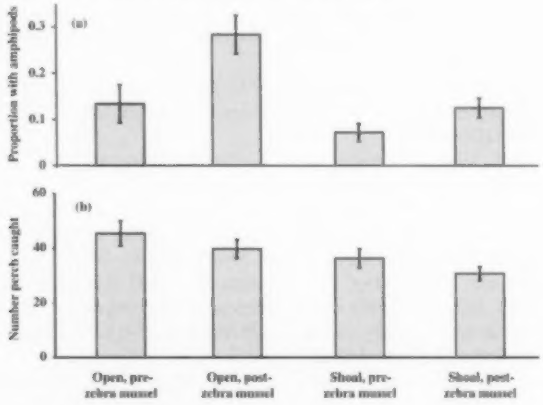
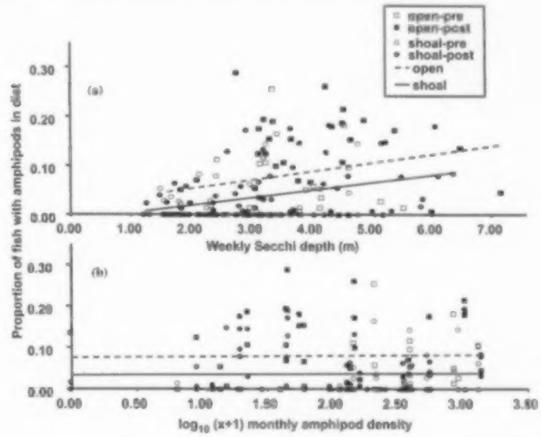


Fig. 5. Proportion of the adult yellow perch that consumed amphipods (arcsine square-root transformed) related to (*a*) weekly Secchi depth and (*b*) monthly amphipod density at two habitat types in Oneida Lake from June to September during pre-zebra mussel (1987–1991) and post-zebra mussel (1992–1999) periods. Data were transformed for statistical analysis and display.



areas experienced an increase in the proportion of the population that captured benthos, though the increase was greater in the open habitat with low zebra mussel density. These results suggest that in the complex lake habitat, and unlike in the laboratory, the negative effects of shell structure reduce, but do not completely eliminate, the potential positive benefits of mussel introduction (high light and high invertebrate density).

Another laboratory study (González and Downing 1999) showed that zebra mussels reduced the consumption rate of bluegill feeding on amphipods (*Echinogammarus ischnus* and *G. fasciatus*), but found no effect on yellow perch during day or night. *Echinogammarus ischnus*, a species that recently invaded the Great Lakes (Witt et al. 1997), is similar in shape and size to *G. fasciatus*, but may differ behaviourally from *G. fasciatus* and may be more vulnerable to yellow perch predation in some structured habitats. *Echinogammarus ischnus* was not present in our study; it has not yet been found in Oneida Lake despite intensive collecting (E.L. Mills and C.M. Mayer, unpublished data).

Our field data showed a positive effect of light penetration on frequency of occurrence of amphipods in yellow perch diets at habitats of both low (open) and high (shoal) zebra mussel density, though there was a great deal of scatter in the relationship. Our laboratory experiments showed no increase in capture rate at two light levels above total darkness. Similarly, adult yellow perch foraging activity has been reported to show a diel pattern, with peak feeding in late evening, a time of relatively low light intensity (Jansen and Mackay 1992). Diehl (1988) further showed that light was more important to feeding rate of European perch (*Perca fluviatilis*) than was habitat complexity. Therefore, yellow perch in systems where zebra mussels have increased water clarity may experience higher rates of benthic foraging, especially at times of low light penetration such as dawn or dusk. Nevertheless, the magnitude of this increase may be limited by the negative effect of increased structural complexity in benthic habitats. Further, light may affect amphipod behaviour differently in habitats of varying complexity.

In our laboratory experiments, *G. fasciatus* activity did not decrease significantly in the presence of zebra mussels, though other studies have reported a decrease in activity of *Gammarus* with increased light in structurally complex habitats (Wallace et al. 1975; Holomuzki and Hoyle 1990). However, amphipod activity did increase significantly with increasing light in the absence of zebra mussels. Similarly, Wallace et al. (1975) suggested that the *Gammarus pseudolimneus* activity level increased in the absence of substrate as they sought darker areas normally found in lake substrate. An aquarium with no sediment or other substrate is obviously an unnatural habitat; however, *G. fasciatus* is semipelagic and does not burrow into sediments as do some amphipods (e.g., Pontoporeiinae; Bousfield 1973), and may increase activity on all flat, unstructured substrates, such as mud and silt, as light level increases. In Oneida Lake on sandy substrates, *G. fasciatus* frequently responds to disturbance by a SCUBA diver with rapid horizontal movement directly above the substrate, but this behaviour has never been observed over zebra mussel encrusted hard substrates (C.M. Mayer, personal observation). Therefore, an increase in amphipod activity with light level may further contribute to the observed increase in frequency of occurrence of amphipods in yellow perch diets at open (low zebra mussel density) sites, but probably not at shoal (high zebra mussel density) sites.

Our data showed no relationship between amphipod density and the number of amphipods captured in any of the habitat types tested in the laboratory or in the field. However, it must be remembered that our index of field densities of amphipods was derived from data collected entirely on soft substrates, which are low zebra mussel density habitats. The lack of a relationship between prey density and capture rate suggests that fish populations will not benefit from the well-documented (Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998) increase in invertebrate densities associated with zebra mussel beds. It is often assumed that there is some relationship between prey density and capture rate, though this relationship (the functional response) may have different forms (Peterman and Gatto 1978). However, most studies dealing with the functional response of fish to prey density have involved pelagic prey. Study results showing an effect of fish presence or density on prey density in complex, benthic habitats have been variable (Thorp 1986), unlike results seen in open water communities (e.g., Carpenter et al. 1985). Our results further suggest that in structurally complex habitats such as the benthos or the littoral zone of lakes there may be only a weak relationship between prey density and capture rates at natural prey densities.

Our laboratory experiments and field data suggest that zebra mussels most strongly affect yellow perch foraging by increasing light levels, a positive effect, whereas the negative effect of structural complexity is less strong. Increased invertebrate density does not appear to positively affect yellow perch foraging. However, the growth rate of adult yellow perch in Oneida Lake did not change after zebra mussel introduction, even though long-term field data show that the frequency of occurrence of both benthic invertebrate and zooplankton prey increased in their diets (Mayer et al. 2000). Apparently the shift in diet has not conferred an energetic advantage upon the yellow perch of Oneida Lake. It is possible that in the post-zebra mussel time period yellow perch expend more time and energy capturing benthic prey, even in open habitats where invertebrates may be clustered in zebra mussel rich microhabitats. This lack of correspondence between diet and growth rate again demonstrates the complexity and unpredictability involved in ecological disturbances such as species introductions.

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Scaled chrysophytes as indicators of water quality changes since preindustrial times in the Muskoka–Haliburton region, Ontario, Canada

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Abstract: Scaled chrysophytes preserved in modern and fossil sediment samples from lakes in south-central Ontario were examined to evaluate changes in water quality since preindustrial times. Redundancy analysis determined that chrysophyte distributions were related to a primary gradient of pH, alkalinity, and ion concentration ($\lambda_1 = 0.26$). A 117-lake reconstruction model from Ontario, the Adirondacks, and northeastern U.S.A. was used to infer the lakewater pH of present-day and preindustrial samples. A comparison of predicted and measured pH values of modern samples, analog matching, and an examination of inferences from triplicate cores in four lakes suggested that the inferences were reliable. Reconstructions indicated that presently acidic lakes (pH < 6) had acidified, whereas lakes with measured pH > 7 had become more alkaline. In comparison to other acid-sensitive regions, however, the overall change was small. The relatively short pH gradient, higher preindustrial pH values, and amount of acid deposition are factors that may explain these trends. Finally, we introduce a novel, multi-indicator reconstruction model, which provides an average of environmental reconstructions from diatom, chrysophyte cyst, and scaled chrysophyte assemblages. This model performed as well or better than the individual inferences when used to predict the pH of modern samples.

Résumé : L'examen des chrysophytes écailleuses conservées dans des échantillons de sédiments récents et fossiles de lacs du centre-sud de l'Ontario nous a permis d'évaluer les changements de la qualité de l'eau depuis l'époque pré-industrielle. Une analyse de redondance indique que la répartition des chrysophytes est reliée à un gradient primaire constitué du pH, de l'alcalinité et de la concentration des ions ($\lambda_1 = 0,26$). Un modèle de reconstitution basé sur 117 lacs de l'Ontario, des Adirondacks et du nord-est des États-Unis a servi à estimer les pH de l'eau des lacs à partir des échantillons des périodes actuelle et pré-industrielle. Une comparaison des valeurs prédites et mesurées des pH des échantillons de sédiments récents, un appariement analogique et un examen des estimations obtenues à partir de trois séries de carottes de sédiments prélevées dans quatre lacs indiquent que les estimations sont fiables. Les reconstitutions montrent que les lacs qui sont actuellement acides (pH < 6) se sont acidifiés depuis la période pré-industrielle, alors que les lacs avec un pH > 7 sont devenus plus alcalins. Cependant, en comparaison avec d'autres régions sensibles à l'acidification, les changements ont, en général, été peu importants; ces tendances peuvent s'expliquer par divers facteurs, dont un gradient relativement restreint des valeurs de pH, des pH plus élevés à l'époque pré-industrielle et l'importance des précipitations acides. Nous présentons enfin un nouveau modèle de reconstitution environnemental basé sur les regroupements de diatomées, de kystes de chrysophytes et de chrysophytes écailleuses; ce modèle fonctionne aussi bien ou même mieux que les méthodes d'estimations individuelles pour prédire le pH d'échantillons de sédiments récents.

[Traduit par la Rédaction]

Introduction

Muskoka–Haliburton is located within the Canadian Precambrian Shield, approximately 200 km north of Toronto, Ont. (Fig. 1). Since the mid-19th century, the water quality of Muskoka lakes has been increasingly threatened by anthropogenic disturbances. These disturbances occur both at a watershed scale, such as the input of nutrients from septic systems (Dillon et al. 1993), and at a regional scale, including the deposition of strong acids from long-range transport (Dillon et al. 1987). Disentangling the relative effects of these factors on water quality is complicated because they may act synergistically in many lakes. Furthermore, changing climatic conditions can play a confounding role (Yan et

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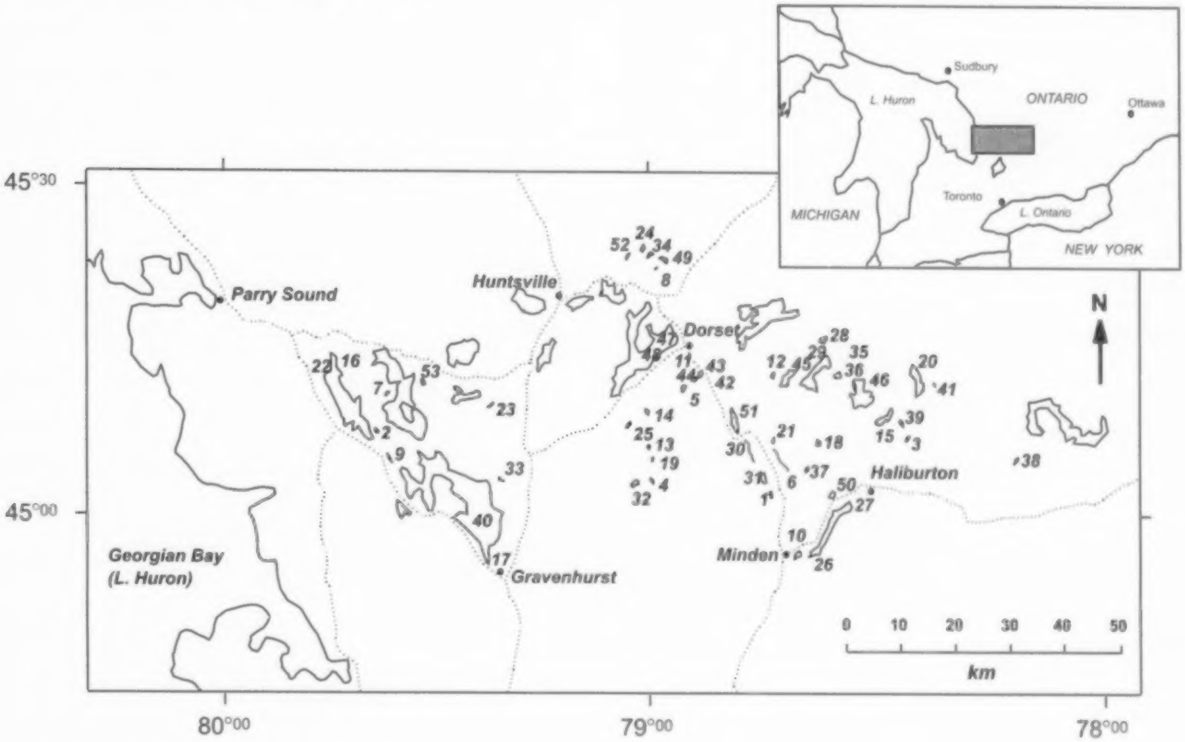
Fig. 1. Map showing the location of the 53 study lakes in the Muskoka–Haliburton region of south-central Ontario, Canada. Numbers represent lake codes that are displayed in Table 1.



al. 1996). Despite growing evidence that water quality may be adversely affected by these disturbances, few studies have attempted to quantify these effects relative to background or preindustrial conditions.

Long-term data and a knowledge of predisturbance conditions are required to assess the effects of environmental stressors on water quality (Smol 1992). The top–bottom paleolimnological approach may be used to obtain regional estimates of environmental change since preindustrial times. Biological assemblages that are preserved in the surface sediments of lakes (top samples) are compared with those from preindustrial (i.e., pre-1850s) samples (bottom samples), providing a measure of environmental change relative to background or "natural" conditions. The top–bottom technique has been used successfully to infer changes in water quality variables (e.g., pH, alkalinity, heavy metals, total phosphorus) in many regions of North America, including Sudbury, Ont. (e.g., Dixit et al. 1992*b*) and the Adirondacks, N.Y. (e.g., Cumming et al. 1992*b*), as well as in other regions (e.g., Sweden, Korsman 1999).

Recently, top–bottom paleolimnological studies in the Muskoka–Haliburton region have been used to infer changes in lakewater pH, total phosphorus (diatoms, Hall and Smol 1996; chrysophyte cysts, Wilkinson et al. 1999), and lakewater oxygen (chironomids, Quinlan et al. 1998). Results from these studies suggest that changes in water quality have been minimal in many of the Muskoka lakes. For example, Hall and Smol (1996) and Wilkinson et al. (1999) determined that the pH and total phosphorus of ~60% of lakes examined had changed less than the root mean squared error (RMSE) of the predictive models since preindustrial times.

Using multiple indicators, paleolimnological studies may provide a more complete understanding of environmental change. Scaled chrysophytes are sensitive indicators of changes in water quality (Smol 1995), and these organisms are an important component of the phytoplankton of lakes in the Precambrian Shield (Siver 1995). The siliceous scales and bristles of scaled chrysophytes are often abundant and well preserved in lacustrine sediments (Smol 1995), and can be reliably identified using a light microscope. Individual taxa have been shown to have well-defined ecological optima and tolerances that can be quantitatively modelled to infer environmental conditions in the past (Siver 1995). Lakewater pH has been shown to be the most important physical–chemical variable influencing scaled chrysophyte assemblages in many of these studies (e.g., Dixit et al. 1999).

In this paper, we explore changes in water quality since preindustrial times in Muskoka–Haliburton lakes, using scaled chrysophytes as indicators of environmental change. First, ordination techniques are used to explore the relationship between scaled chrysophyte assemblages and measured environmental variables from 53 lakes in south-central Ontario. Second, we explore regional trends in lakewater pH since preindustrial times. Monitoring studies in the Muskoka–Haliburton region suggest that many lakes have been adversely affected by the deposition of strong acids (e.g., Stoddard et al. 1999). However, other paleolimnological evidence suggests that these impacts have been small since preindustrial times (Hall and Smol 1996; Wilkinson et al. 1999). Scaled chrysophytes have been shown to be sensitive indicators of lake acidification (Smol 1995), often showing inferred pH changes greater than those from other indicators (e.g., diatoms). Finally, we introduce a new, multi-indicator reconstruction model that may be used to better understand changes in lakewater pH in the Muskoka–Haliburton region. We discuss how this model, which incorporates information from diatom (Hall and Smol 1996) and chrysophyte (Wilkinson et al. 1999; this study) inference models, may be of particular interest to lake managers.

Methods

Study region

The Muskoka–Haliburton region of south-central Ontario is underlaid with Precambrian granitic bedrock of the Canadian Shield (Jeffries and Snyder 1983). A marble intrusion, found in the eastern portion of the study area, underlies 12 of the study lakes. Soils are generally shallow and acidic, although thicker deposits of clay, sand, or gravel occur locally (Chapman and Putnam 1984). Much of this region is characterized by secondary mixed-deciduous and coniferous forests, following widespread deforestation in the mid- to late-1800s (Hall and Smol 1996). Because of the rough topography, thin soils, and cool climate, agriculture is marginal in the region. Presently, human activity consists primarily of recreational activities associated with seasonal cottages, and rural municipalities.

Field and laboratory work

In the fall of 1992, 54 lakes in the Muskoka–Haliburton region were selected for study (Hall and Smol 1996) (Table 1). Sediment cores were extracted from the deepest basin of each lake using a Glew (1989) gravity corer fitted with a 6.35-cm internal diameter Lucite tube, and sectioned at the lakeshore into stratigraphic sections using a Glew (1988) vertical extruder. Two sediment sections were examined: the top centimetre (present-day lake conditions), and a 1-cm interval taken at a minimum core depth of 20 cm (preindustrial lake conditions). Although the precise date of the bottom sample of each core is not known, radiometric ^{210}Pb dating of other cores from the south-central Ontario region has shown that background conditions (i.e., >150 years) are typically reached at core depths of 15–20 cm (e.g., Clerk et al. 2000).

Water chemistry data were collected from 1990 to 1992 by personnel of the Ontario Ministry of the Environment (Hall and Smol 1996). All variables, excluding total phosphorus, were calculated as volume-weighted averages of ice-free concentrations for this time period. Total phosphorus measurements were calculated as spring overturn values. Morphometric variables, including maximum depth (Z_{max}), surface area (SA), watershed area (WA), and a volume-weighted measure of lakeshore development (no. cottages·SA^{-1}·Z_{max}^{-1}) were also calculated (Wilkinson et al. 1999), bringing the total number of physical–chemical variables to 18 (Table 2).

Microscope slides were prepared following the standard acid-digestion techniques described in Hall and Smol (1996). A minimum of 300 chrysophyte scales were enumerated along transects at 1500× (100× objective, 15× ocular lens) using a Leica DMRB light microscope with differential-interference-contrast optics. Scales of a few taxa were grouped into broader taxonomic categories because of difficulty in identifying these scales to the species level using a light microscope. For example, unidentifiable small and mid-sized scales were grouped into the categories *Mallomonas* "small" and "medium", respectively. These groups were relatively rare, with abundances of no greater than three or six percent in any lake.

Statistical analysis

In total, 32 taxa were identified in the top and bottom sediment samples of the study lakes. Eight taxa were considered rare as they did not reach a relative abundance of greater than 1% in any sample and were eliminated from subsequent analyses (Table 3). For statistical analyses, species data were square-root transformed to reduce the impact of very abundant taxa. Detrended correspondence analysis (DCA), with detrending by segments, was used to determine the maximum amount of variation in the species data (Hill and Gauch 1980). Owing to the short gradient length of the first DCA axis (1.44 standard deviation units), linear ordination techniques were used to determine the main directions of variation in the chrysophyte data (principal components analysis, PCA), and to explore the relationship between scaled chrysophyte assemblages and the 18 environmental variables (redundancy analysis). Ordinations were based on a covariance matrix between the chrysophyte variables, and performed on square-root transformed species data without downweighting of rare taxa.

A forward selection step was used with redundancy analysis (RDA) to reduce the problem of colinearity in the explanatory variables. Environmental data were screened for normality, and log or square-root transformed if appropriate, to meet the assumptions of parametric statistical analyses. Monte Carlo permutation tests (999 permutations) were used (*i*) to test the significance of each forward selected variable, and (*ii*) to test the significance of the first and second RDA axes defined by the forward selected environmental variables. The statistical package CANOCO version 4 (ter Braak and Šmilauer 1998) was used for the ordinations.

The pHs of modern and fossil samples were inferred using a 117-lake reconstruction model, which included lakes from this study (Hall and Smol 1996), Adirondack Park (Cumming et al. 1992*a*), and northeastern U.S.A. (Dixit et al. 1999). The 117-lake model was used in place of an intraregional model developed using the 53 lakes in south-central Ontario. The 53-lake model was found to be unreliable when reconstructing the pH of fossil samples, as many had species assemblages that were not well represented in the modern samples (Paterson et al. 2002). A strong relationship between measured pH and DCA axis 1 scores (r = 0.89) determined that pH tracked the main direction of variation in the 117-lake training set. Detrended canonical correspondence analysis (DCCA), with pH as the sole constraining variable, suggested that unimodal modelling techniques were appropriate for inferring the pH of modern and fossil samples (Paterson et al. 2002). A weighted averaging partial least squares (WA-PLS) regression and calibration model (2 components) was used to reconstruct the pH of south-central Ontario samples, using the program CALIBRATE (S. Juggins, Department of Geography, University of Newcastle, U.K., and C.J.F. ter Braak, Institute of Forestry and Nature Research, P.O. Box 100, NL-6700 AC Wageningen, The Netherlands).

Variability as a result of sampling, counting, and random errors may influence the reconstructions in this study. A number of tests were performed to assess the reliability of the pH inferences. First, the 117-lake model was used to predict the pH of the modern samples. The jack-knifed coefficient of determination and residual structure of the comparison were examined. Second, analog matching was applied on square-root transformed data to determine whether fossil species assemblages were well represented in the modern samples of the 117-lake training set. Using the Bray–Curtis coefficient (Bray and Curtis 1957), a distribution of minimum dissimilarities was calculated through comparisons among modern samples. The Bray–Curtis coefficient was selected as it is intuitively simple and gives equal importance to all taxa. Similar results were achieved using other coefficients (e.g., Euclidean). When compared to modern samples, fossil samples with minimum dissimilarities greater than the extreme 5% of modern distribution were considered to have poor analogs. Analog matching was performed using the statistical program ANALOG version 1.6 (J.M.

Table 1. Latitude, longitude, and the measured pH of the 53 study lakes.

Lake code	Lake name	Latitude (N)	Longitude (W)	pH
1	12 Mile	45°01′	78°43′	7.0
2	Bass	45°07′	79°42′	6.3
3	Basshaunt	45°07′	78°28′	6.7
4	Bigwind	45°03′	78°04′	6.3
5	Blue Chalk	45°11′	78°56′	6.7
6	Boshkung	45°04′	78°44′	6.9
7	Bruce	45°11′	79°40′	6.8
8	Buck	45°22′	79°00′	6.5
9	Butterfly	45°05′	79°38′	7.0
10	Canning	44°57′	78°38′	7.3
11	Chub	45°13′	78°59′	5.7
12	Clear	45°11′	78°43′	5.8
13	Crosson	45°05′	78°02′	5.6
14	Dickie	45°09′	79°05′	5.9
15	Eagle	45°08′	78°29′	7.2
16	Frazer Island (L. Joseph)	45°15′	78°46′	6.7
17	Gravenhurst Bay (L. Muskoka)	44°56′	79°24′	7.2
18	Green	45°07′	78°37′	7.2
19	Gullfeather	45°06′	79°01′	5.8
20	Haliburton	45°13′	78°25′	7.0
21	Hall's	45°06′	78°44′	6.5
22	Hamer Bay (L. Joseph)	45°13′	79°46′	6.6
23	Hammel Bay (Three Mile L.)	45°10′	79°27′	7.2
24	Harp	45°23′	78°08′	6.4
25	Heney	45°08′	79°06′	5.8
26	Kashagawigamog North Basin	45°01′	78°34′	7.2
27	Kashagawigamog South Basin	45°01′	78°34′	7.2
28	Kelly	45°15′	78°37′	6.2
29	Kennisis	45°13′	78°39′	6.3
30	Kushog North Basin	45°08′	78°50′	6.5
31	Kushog South Basin	45°06′	78°48′	6.5
32	Leech	45°03′	79°06′	6.2
33	Leonard	45°04′	79°27′	6.0
34	Little Clear	45°24′	79°01′	6.8
35	Little Kennisis	45°15′	78°36′	6.1
36	Little Redstone	45°13′	78°34′	6.3
37	Maple	45°06′	78°40′	7.1
38	McKay	45°04′	78°10′	6.3
39	Moose	45°09′	78°28′	7.2
40	Muskoka Bay (L. Muskoka)	45°57′	79°24′	7.1
41	Oblong	45°11′	78°26′	7.1
42	Plastic	45°11′	78°50′	5.7
43	Red Chalk East Basin	45°11′	78°56′	6.5
44	Red Chalk Main Basin	45°11′	78°56′	6.3
45	Red Pine	45°12′	78°42′	6.3
46	Redstone	45°12′	78°32′	6.5
47	Roothog Island (Lake of Bays)	45°15′	79°00′	6.8
48	Seagull Rock (Lake of Bays)	45°15′	79°00′	6.7
49	Solitaire	45°24′	79°01′	6.7
50	Soyer's	45°01′	78°37′	7.0
51	St. Nora	45°09′	78°50′	6.3
52	Walker	45°24′	79°05′	6.7
53	Young	45°12′	79°33′	6.7

Line, University of Cambridge Computer Library, Pembroke Street, Cambridge CB2 3QG, U.K., and H.J.B. Birks, Botanical Institute, University of Bergen, Allégaten 41, N-5007 Bergen, Norway). Third, triplicate cores were collected from the deepest basin of four of the lakes (Bass (2), Crosson (13), Dickie (14), and Little Clear (34)). Top and bottom samples were enumerated for each of the cores, and pH inferences were compared.

To test whether species changes were related to changes in pH, a

Table 2. Minimum, maximum, and mean values of 18 physical–chemical variables from the 53 study lakes.

Variable	Minimum	Maximum	Mean
pH	5.6	7.3	6.6
Alkalinity (mg·L^{-1} CaCO$_3$)	0.4	23.0	6.2
Conductivity (µS·cm^{-1})	22.2	87.0	43.3
DOC (mg·L^{-1})	1.7	5.8	3.5
[Ca] (mg·L^{-1})	1.8	14.2	4.3
[Mg] (mg·L^{-1})	0.5	2.3	1.0
[Na] (mg·L^{-1})	0.5	9.0	1.8
[K] (mg·L^{-1})	0.2	1.0	0.6
[SO$_4$] (mg·L^{-1})	4.2	9.4	7.5
[NH$_3$] (µg·L^{-1})	5.0	83.9	20.2
[NO$_3$] (mg·L^{-1})	2.0	247.0	103.6
[TN] (mg·L^{-1})	140.0	380.0	236.2
[TP] spring overturn (µg·L^{-1})	2.7	24.3	7.3
[Si] (mg·L^{-1})	0.1	1.9	0.9
Surface area (ha)	10.9	1675.0	274.5
Watershed area (ha)	127.6	89 658.0	12 388.5
Maximum depth (m)	5.8	82.4	31.9
No. cottages·SA^{-1}·$Z_{max}$$^{-1}$ (no.·ha^{-1}·m^{-1})	0.0	1.3	0.6

Note: No. cottages·SA^{-1}·$Z_{max}$$^{-1}$ is an index of volume-weighted lakeshore development (Wilkinson et al. 1999).

Table 3. The number of occurrences, the effective number of occurrences (Hill's N2), mean, and maximum relative abundances of the 24 taxa that occurred in at least three lakes and had a relative abundance of >1% in at least one of the 53 study lakes.

Taxon code	Taxon	No. occurrences	N2	Mean	Maximum
A	*Mallomonas acaroides* var. *muskokana*[a] Nicholls	21	9.35	0.71	7.13
B	*M. akrokomas* Ruttner in Pascher	34	22.66	0.52	2.34
C	*M. allorgei* (Defl.) Conrad	9	3.39	0.16	4.18
D	*M. caudata* Ivanov em. Krieger	53	30.22	4.01	19.56
E	*M. crassiaquama* (Asmund) Fott	53	37.21	8.93	24.26
F	*M. duerrschmidtiae* Siver, Hamer & Kling	52	17.20	6.54	43.24
G	*M. elongata* Reverdin	36	23.53	0.57	3.17
H	*M. hamata* Asmund	50	28.87	3.83	14.50
I	*M. heterospina* Lund	20	9.96	0.24	2.49
J	*Mallomonas* "medium" group[b]	35	16.80	0.55	3.43
K	*M. pseudocoronata* Prescott	52	15.40	3.34	34.24
L	*M. punctifera* Korsh.	27	16.88	0.44	2.74
M	*Mallomonas* "small" group[c]	47	29.34	0.93	3.44
N	*M. tonsurata* Teiling em. Krieger	46	23.51	1.09	6.34
O	*M. torquata* Asmund and Cronberg	49	29.76	0.67	2.97
P	*Synura curtispina* (Petersen & Han.) Asmund	40	14.04	1.82	13.79
Q	*S. echinulata* Korsh.	52	18.13	8.45	50.87
R	*S. petersenii* Korsh.	53	36.78	28.13	72.24
S	*S. sphagnicola* Korsh.	47	20.14	13.99	67.66
T	*S. spinosa* Korsh.	52	28.50	4.56	17.98
U	*S. uvella* Stein em. Korsh.	45	17.64	4.33	32.84
V	*Chrysosphaerella* Lauterborn[d]	52	19.12	4.95	36.03
W	*Paraphysomonas* deSaedeleer	32	22.48	0.33	1.69
X	*Spiniferomonas* Takahashi	49	32.93	0.67	2.74

[a] May include the nominate variety in some samples.

[b] Includes unidentified *Mallomonas* scales larger than *Mallomonas* "small", e.g., *M. intermedia* Kisselew and *M. corymbosa* Asmund & Hillard.

[c] Includes small unidentified *Mallomonas* scales, e.g., *M. galeiformis* Nicholls.

[d] Includes *Chrysosphaerella brevispina* Korshikov and *C. longispina* Lauterborn em. Nicholls.

Bray–Curtis dissimilarity was calculated between the modern and fossil sample of each lake and compared to the absolute value of the inferred pH change. Lakes that had both a Bray–Curtis dissimilarity greater than the mean value (0.41) and pH change less than the mean change (0.28 pH units) were considered outliers. These lakes exhibited species changes that were not strongly related to changes in pH.

A multi-indicator reconstruction model for inferring lakewater pH was calculated by combining the diatom (Hall and Smol 1996), chrysophyte cyst (Wilkinson et al. 1999), and scaled chrysophyte (this study) inferences of pH in two ways: (*i*) a mean weighted by the cross-validated coefficient of determination (r^2) of each model, which was calculated from comparisons of predicted and observed pH, and (*ii*) a mean weighted by one minus the cross-validated RMSE, which was calculated separately for each paleolimnological indicator. The performance of the multi-indicator models was evaluated by comparing the predicted inferences of the modern samples with measured values.

Results and discussion

A total of 32 scaled chrysophyte taxa or groups were identified in the surface sediment of the study lakes. Chrysophyte scales were extremely rare in the surface sediment of Three Mile Lake; therefore, this lake was excluded from further analyses. In general, the present-day sediment samples were dominated by taxa of the genus *Synura*. In 41 of the 53 lakes examined, the relative abundance of *Synura* was greater than 50%. *Synura* accounted for greater than 75% of the species assemblage in 16 of the lakes. The most abundant chrysophyte taxon in the modern samples was *Synura petersenii*, occurring at an average relative abundance of 28% across all lakes, and reaching relative abundances of greater than 30% in 20 of the lakes. *Synura sphagnicola* and *Synura echinulata* also contributed to the high total *Synura* abundances, with average relative abundances of 14% and 8%, respectively. By comparison, the most abundant *Mallomonas* taxa in the surface samples were *Mallomonas crassisquama* and *Mallomonas duerrschmidtiae*, with average relative abundances of 9% and 7%, respectively.

A comparison of modern and fossil sediment intervals suggested that there has been a regional shift from a *Mallomonas*- to a primarily *Synura*-dominated species assemblage (Figs. 2*a*, 2*b*). *Mallomonas duerrschmidtiae* and *M. crassisquama* were the most abundant taxa in the preindustrial time period, occurring at mean relative abundances of 26% and 15%, respectively, across all lakes (Fig. 2*b*). *Synura petersenii*, the most abundant *Synura* taxon in both the present-day and preindustrial time periods, was found at a mean relative abundance of approximately 8% in the fossil samples.

Poor preservation or differential dissolution of siliceous material may discredit the value of paleoecological inferences. In some environments, such as lakes with very low sediment accumulation or high pH, preservation may be compromised (e.g., Flower 1993). In this study, however, the preservation of siliceous material was found to be excellent in the modern samples of all lakes, and in the majority of fossil samples. Furthermore, the thinly silicified remains of other organisms, such as the spines and finer patterning on the surface of chrysophyte cysts, were well preserved. Five of the fossil samples showed low abundances or evidence of dissolution (Bruce (7), Butterfly (9), Frazer Island (16), Heney (25), and Plastic (42)). To avoid potential biases, these lakes were excluded from the calculation of pH changes since preindustrial times.

The relationship between scaled chrysophytes and environmental variables

Eigenvalues ($\lambda_1 = 0.31$, $\lambda_2 = 0.19$) of the first and second PCA axes accounted for 50.2% of the variation in the species data. The strength of the first axis suggested that the distribution of chrysophyte taxa in the modern samples was related to a strong primary gradient. In an exploratory RDA, including all of the measured environmental variables, the first ($\lambda_1 = 0.28$) and second ($\lambda_2 = 0.14$) axes explained 42.1% of the cumulative variance in the species data. Forward selection produced six environmental variables (pH, DOC, log[Na], [SO_4], log[NH_3], and [NO_3]) that explained significant directions of variation in the chrysophyte data. Constrained to the forward-selected environmental variables, the eigenvalues of the first ($\lambda_1 = 0.26$) and second ($\lambda_2 = 0.12$) RDA axes were significant ($P \leq 0.01$), and explained 37.9% of the cumulative variation in the chrysophyte data. Species–environmental correlations of the first two RDA axes were high (0.92 and 0.81), suggesting that the forward-selected environmental variables explained major directions of variation in the species data.

The RDA axis 1 captured a gradient of pH and pH-related variables (Table 4; Fig. 3). Alkalinity, conductivity, and ionic concentration ([Mg], [K], [Ca], and [SO_4]) were highly correlated with pH along the first axis (Fig. 3*a*). This axis may reflect the importance of acidic deposition on the chemistry and biology of lakes in the Muskoka–Haliburton region (Wilkinson et al. 1999). In general, oligotrophic lakes of low conductivity and poor buffering capacities have been most susceptible to acidification (Hall and Smol 1996). RDA axis 1 effectively separated low-conductivity, acidic lakes (Fig. 3*c*: Chub (11), Clear (12), Crosson (13), Dickie (14), Heney (25), and Plastic (42)) from some of the more alkaline lakes (Fig. 3*c*: Eagle (15), Moose (39), and Oblong (41)). All of the lakes found within the marble inclusion were clustered towards the more alkaline end of the first RDA axis (Fig. 3*c*).

Similarly, chrysophyte taxa that commonly occur at higher relative abundances in more acidic environments (Siver 1995), such as *Mallomonas acaroides* var. *muskokana* and *S. sphagnicola*, were positioned at the acidic end of the pH gradient (Fig. 3*b*). *Mallomonas hindonii*, an excellent indicator of low pH (e.g., Cumming et al. 1992*a*), did not meet the abundance criteria in these lakes, and therefore was not included in the ordinations (see Methods). The species *Synura uvella* and *Synura curtispina* were positioned at the alkaline end of the first RDA axis (Fig. 3*b*). Interestingly, *S. echinulata* was also positioned at the alkaline end of the gradient, despite evidence that this species is largely acidophilous in its preference for pH (Siver 1995). This finding is supported by Cumming et al. (1992*a*) and Dixit et al. (1999), who reported a bimodal response of *S. echinulata* along a gradient of pH from lakes in Adirondack Park and northeastern North America, respectively. Owing to the absence of strongly acidic lakes in this study (Table 2), the more acidophilous form of the taxon may have been underrepresented in the lake set. It is possible that the taxon identified here is actually *Synura leptorrhabda* (Asmund) Nicholls comb. nov., which has been shown to occur in south-central Ontario lakes (Nicholls and Gerrath 1985). This taxon may only be reliably separated from *S. echinulata* using an electron microscope. Previous reports of this taxon have given little indication regarding its ecological preferences, although it has been shown to occur in lakes within the Canadian Shield (Kling and Kristiansen 1983).

The importance of pH to the distribution of scaled chryso-

Fig. 2. The relative abundance of dominant scaled chrysophyte taxa (>10% in one sample) in present-day (open bars), and preindustrial (closed bars) sediment samples that have (*a*) increased or (*b*) decreased in mean abundance since preindustrial times. The inferred pH change is shown in (*c*), where open bars represent lakes in which fossil samples were determined to have poor moderns analogs. Dotted vertical lines in (*c*) denote plus or minus the root mean squared error (RMSE) of prediction. Lakes are arranged in order of increasing measured pH (in parentheses).

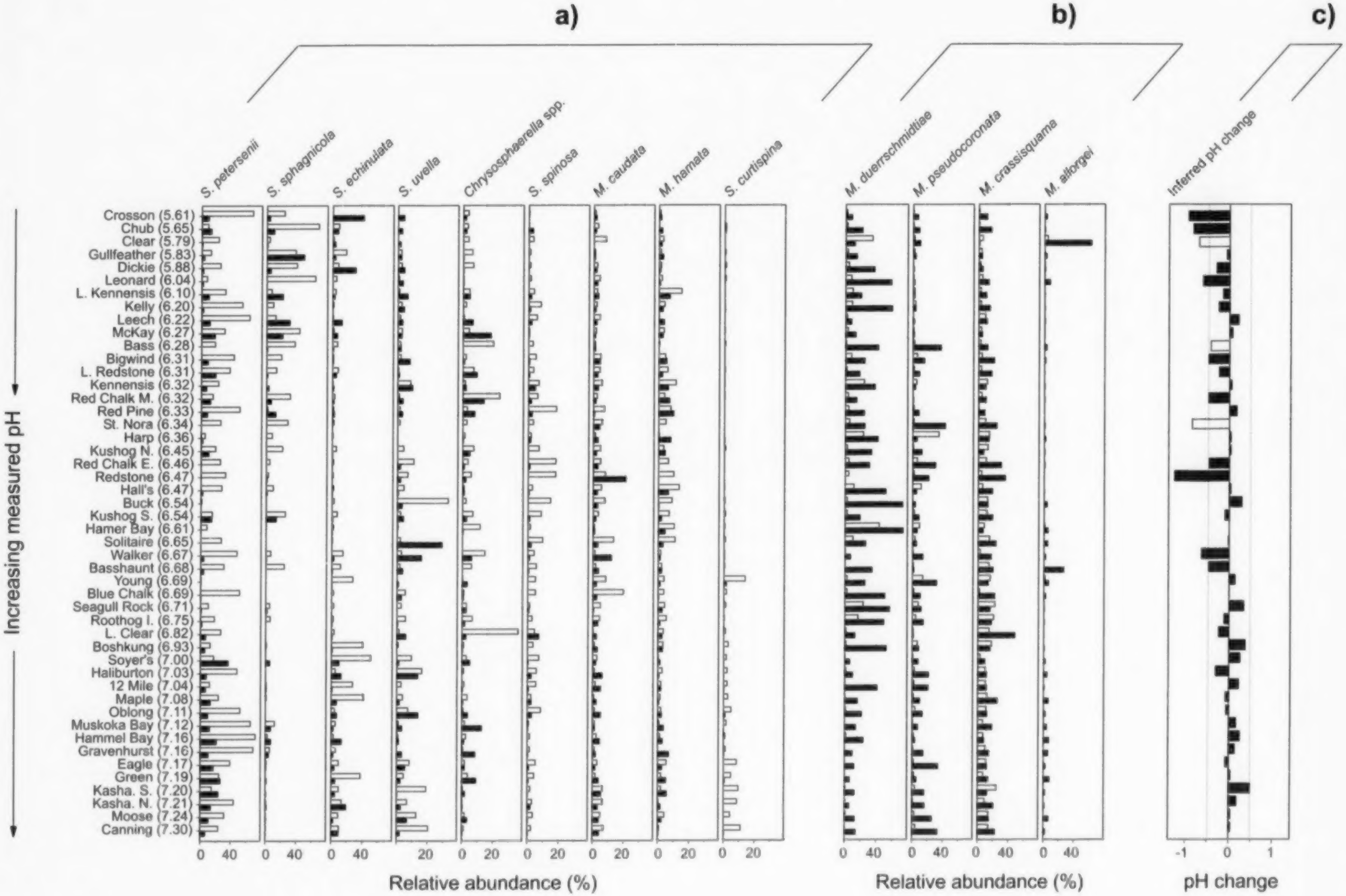
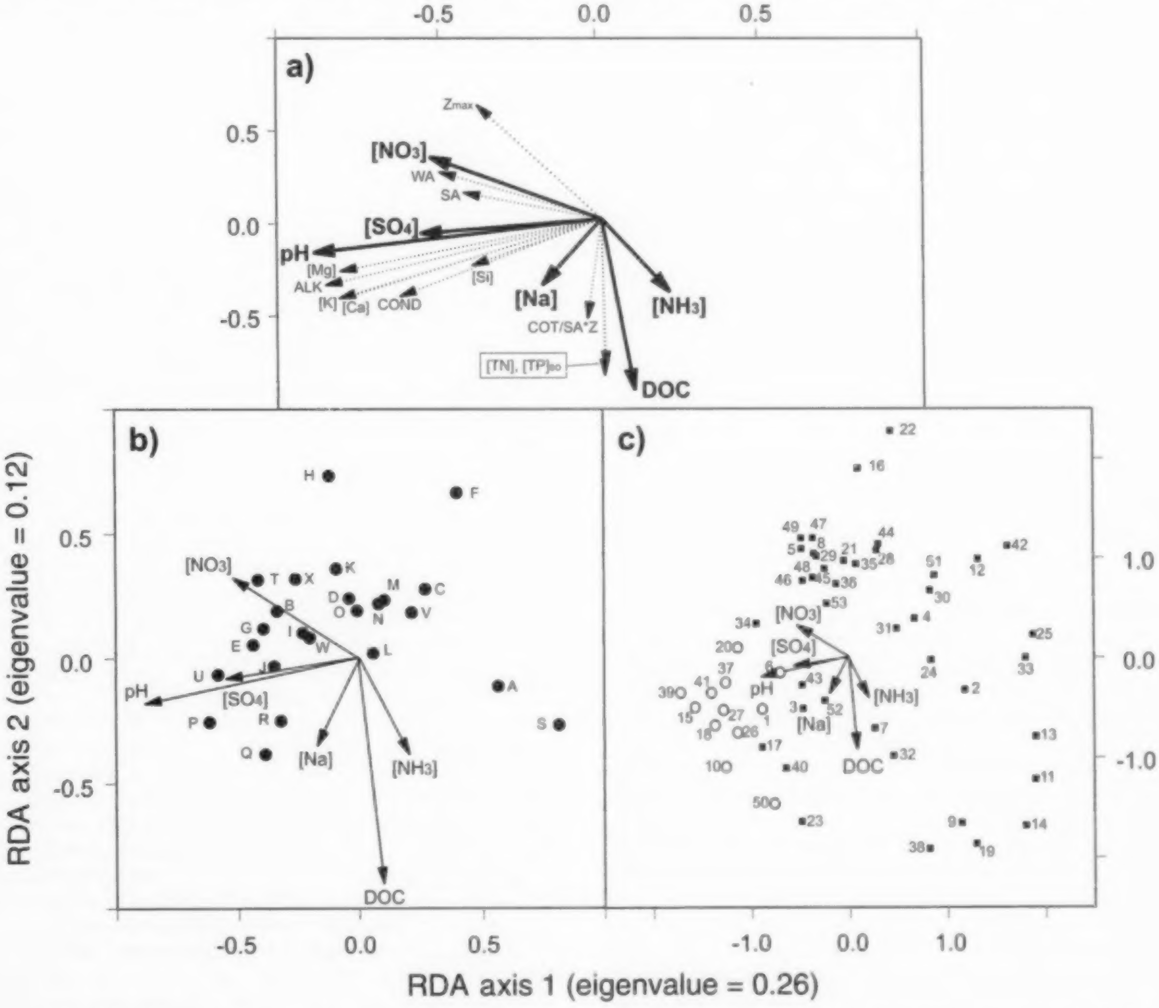


Table 4. Canonical coefficients, approximate *t*-test values, and intraset correlations of the environmental variables for each of the first three redundancy analysis (RDA) axes.

	Canonical coefficients			*t* values			Intraset correlations		
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
pH	−1.1	−0.14	0.27	−12.69*	−0.92	0.95	−0.8	−0.15	−0.19
DOC	0.08	−0.74	−0.06	1.12	−5.94*	−0.26	0.09	−0.72	−0.03
log[Na]	0.47	−0.15	−0.63	5.31*	−0.99	−2.11*	−0.16	−0.27	−0.31
$[SO_4]$	−0.11	−0.44	−0.25	−1.24	−2.91*	−0.85	−0.5	−0.1	−0.14
$\log[NH_3]$	−0.21	−0.14	0.93	−2.86*	−1.11	3.76*	0.18	−0.3	0.48
$[NO_3]$	−0.2	0.56	0.36	−2.07*	3.45*	1.13	−0.47	0.25	−0.17

Note: DOC, dissolved organic carbon; *, significant at $p \le 0.05$.

Fig. 3. Redundancy analysis (RDA) ordination plot showing (*a*) the forward selected (solid lines) and passive (dotted lines) environmental variables, (*b*) the scaled chrysophyte taxa, and (*c*) the 53 study sites in relation to forward selected environmental variables. Site and taxon codes are found in Tables 1 and 3, respectively. Open circles in (*c*) represent lakes situated on marble intrusion.



phytes has been well documented in other studies (Smol 1995). For example, in a study of 71 lakes in the Adirondack Mountains, N.Y., pH and related variables (e.g., monomeric aluminum) were found to be important variables influencing the distribution of chrysophyte taxa (Cumming et al. 1992*a*). A recent, comprehensive study of the relationship of scaled chrysophytes to environmental variables from surface samples of 217 lakes in northeastern U.S.A. determined that pH was the most important variable influencing species distributions (Dixit et al. 1999). In the south-central Ontario lakes, conductivity was strongly correlated to pH along the first RDA axis, and has been identified as an important variable influencing chrysophyte populations in other studies. Siver (1993) reported a good relationship (apparent $r^2 = 0.87$) between observed and chrysophyte-inferred conductivity values in an analysis of 28 lakes in Connecticut (mean conductivity range 28–294 $\mu S \cdot cm^{-1}$ with 13 lakes greater than 100 $\mu S \cdot cm^{-1}$). The comparatively narrow gradient of conductivity observed in the Muskoka–Haliburton lake set (22–87 $\mu S \cdot cm^{-1}$) is too short to obtain meaningful estimates of the ecological optima and tolerances of the chrysophyte taxa.

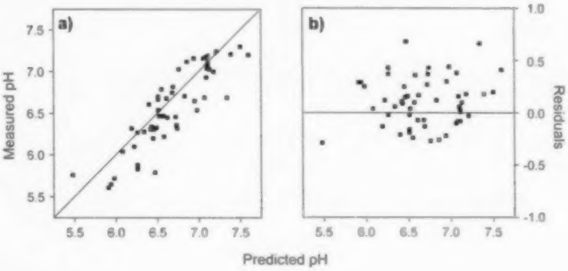
Gradients of dissolved organic carbon (DOC), trophic variables (total nitrogen [TN], and total phosphorus at spring overturn [TP]so), maximum depth, and an index of volume-weighted lakeshore development (no. cottages$\cdot SA^{-1} \cdot Z_{max}^{-1}$, see Methods) were captured by the second RDA axis (Table 4; Fig. 3*a*). The ordination separated shallow, more productive lakes from deeper, less productive lakes. Furthermore, the second axis separated naturally acidic lakes with higher concentrations of DOC (e.g., Gullfeather (19)) from clear, acidic lakes that have acidified as a result of anthropogenic influences (e.g., Plastic (42)). *Mallomonas hamata* and *M. duerrschmidtiae* were positioned at the low end of the DOC–nutrient gradient, indicating that these taxa were most common in deeper, oligotrophic lakes (Fig. 3*b*). This is supported by Siver (1991), who reported these taxa at higher abundances in oligotrophic or mesotrophic habitats with low total phosphorus. With the exception of *Synura spinosa*, *Synura* spp. were more common in shallower lakes, characterized by higher DOC and nutrient levels (Fig. 3*b*). This was true of taxa independent of their positioning along the pH gradient (e.g., *S. sphagnicola* and *S. curtispina*). DOC was highly correlated with trophic variables ([TN] and [TP]so) along the second RDA axis, and consequently the data did not allow us to separate the relative importance of DOC and trophic variables to the distribution of chrysophyte taxa.

Assessing the reliability of the pH reconstructions

To test the ability of the 117-lake model to reconstruct the pH of Ontario lakes, the WA-PLS model was used to predict the measured pH of the 53 modern samples. There was a strong relationship between predicted and measured pH, as inferred using the WA-PLS model (Fig. 4). An examination of the residual structure of the relationship suggested that the 117-lake model tended to overestimate the pH of the Ontario samples. However, this bias was constant along the pH gradient (Fig. 4), suggesting that reliable inferences of pH change (inferred modern pH – inferred fossil pH) could be made.

A second test of the reliability of the pH inferences was analog matching, which determined that only four fossil samples had species assemblages that were poorly represented in the 117-lake training set. The fossil sample of one of these lakes (Clear (12)) was dominated by the chrysophyte *Mallomonas allorgei*, a taxon that is poorly represented in modern samples of many regions of North America (Siver 1991). A second poor analog (Solitaire (49)) had an unusual species assemblage codominated by *S. uvella* and *M. duerrschmidtiae*, taxa that do not typically occur together in high abundances in either the 53-lake and 117-lake training sets.

Fig. 4. Relationship between (*a*) measured and predicted pH (r^2_{jack}, jack-knifed coefficient of determination = 0.76), and (*b*) the residual structure, for modern samples from 53 lakes in south-central Ontario. Predicted values were calculated using a 117-lake weighted averaging partial least squares (WA-PLS) model, which includes lakes from Ontario (Hall and Smol 1996), Adirondack Park (Cumming et al. 1992*a*), and northeastern U.S.A. (Dixit et al. 1999). Diagonal line in (*a*) represents a 1:1 relationship.



A comparison of pH inferences from modern and fossil samples of triplicate cores suggested that the variability among replicates was low (Fig. 5). In two lakes that have shown a significant change in pH since preindustrial times, the variation between top and bottom inferences was greater than the variation among replicates (Fig. 5). Collectively, these results suggest that pH inferences from scaled chrysophyte assemblages examined in sediment cores extracted from the deep basin of lakes are reproducible, and the pH of the Muskoka lakes can be reliably inferred.

In modern training sets, ordination techniques can be used to determine if an environmental variable of interest tracks the main direction of variation in the species data (Birks 1995). However, these comparisons are rarely made with fossil assemblages, and have yet to be used in top–bottom paleolimnological studies. To determine if pH tracked an important direction of variation in the species data through time, we compared the absolute value of inferred pH change with a measure of species dissimilarity (i.e., Bray–Curtis coefficient). Across lakes, a moderate relationship existed between Bray–Curtis dissimilarities and the inferred pH change ($r = 0.56$, $n = 48$, $p < 0.001$), further validating the pH reconstructions, and suggesting that pH was an important variable related to species changes (Fig. 6). However, 10 lakes exhibited species changes that were not strongly related to inferred changes in lakewater pH (see criteria in Methods) (Fig. 6). The chrysophyte *S. petersenii* dominated the species assemblage of five of these lakes. Interestingly, *S. petersenii* increased in relative abundance in all but four lakes since preindustrial times, and presently is the most abundant scaled chrysophyte in approximately half of the lakes.

Changes in lakewater pH since preindustrial times

Our findings suggest that changes in lakewater pH have been small in the study lakes. Approximately 80% of the lakes showed pH changes less than the prediction error of the scaled chrysophyte inference model (Fig. 2*c*). Similar re-

Fig. 5. Inferred pH values from triplicates of modern and pre-industrial sediment samples for four lakes in south-central Ontario. Points represent inferred values and error bars represent plus or minus the root mean squared error (RMSE) of the inference model.

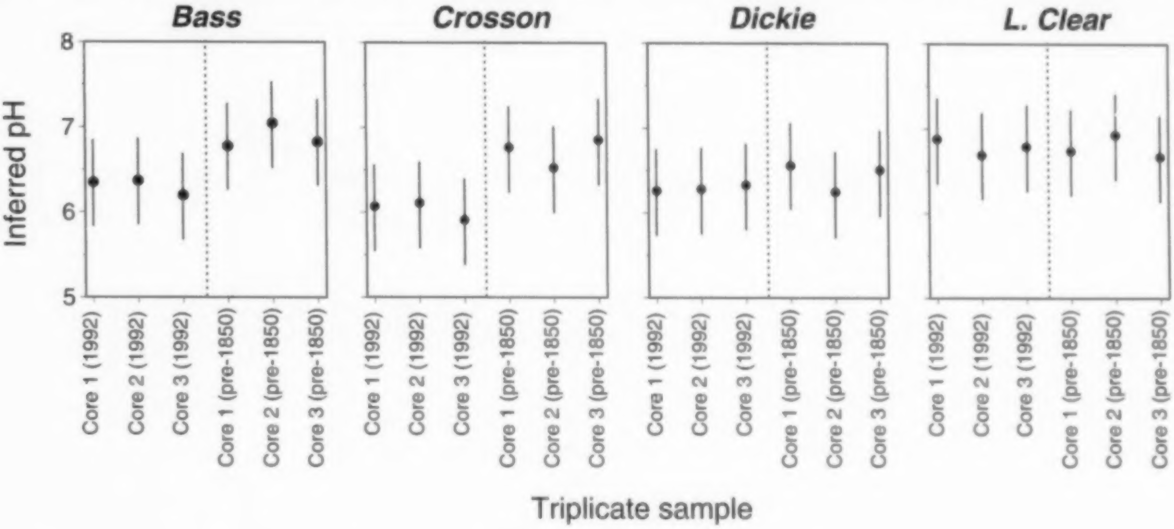
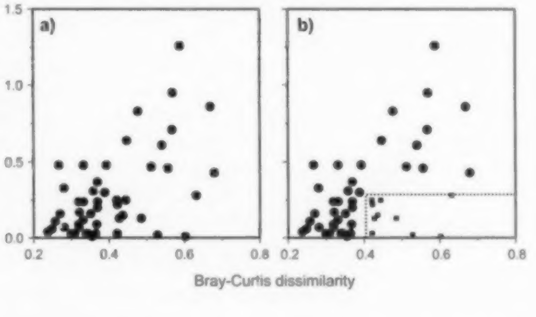


Fig. 6. Scatter-plots of the absolute value of the inferred pH change and the Bray–Curtis dissimilarity of species assemblages since preindustrial times for 48 lakes in south-central Ontario. Plot (*a*) includes the 48 lakes with modern and fossil pH reconstructions. Plot (*b*) is identical to plot (*a*) but differentiates lakes with chrysophyte species changes that are not strongly related to changes in inferred lakewater pH (squares). Removal of these lakes improves the correlation of inferred pH change and Bray–Curtis dissimilarity from $r = 0.56$ to 0.76 ($n = 48$ and 38, respectively).



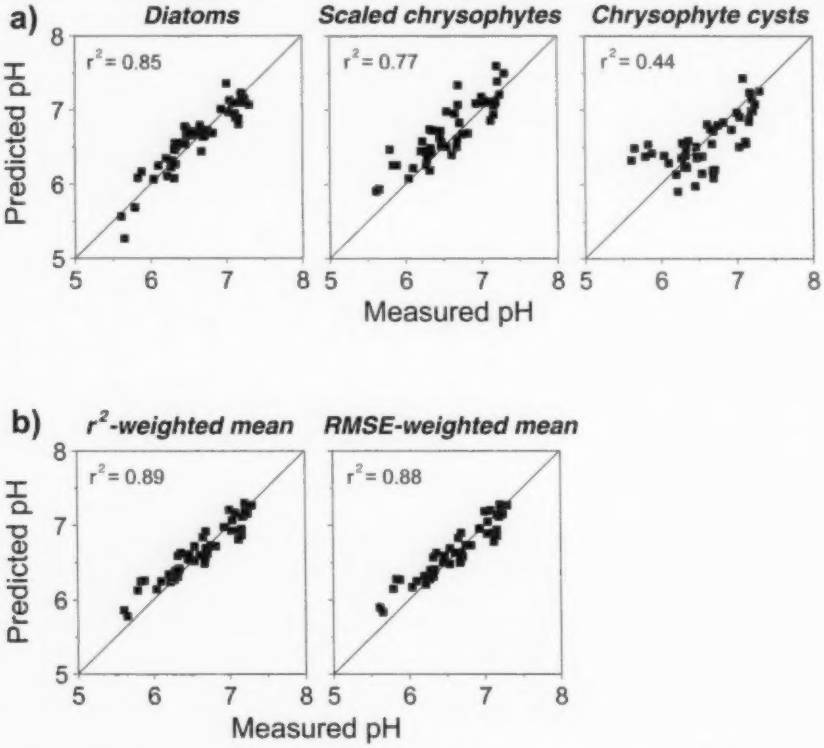
sults have been reported using other paleolimnological indicators. For example, greater than 60% of the study lakes showed nonsignificant pH changes as inferred from both diatom (Hall and Smol 1996) and chrysophyte cyst (Wilkinson et al. 1999) inference models.

Although the magnitude of pH change was not significant (i.e., greater than prediction error of model), there were regional trends with respect to the direction of change in many lakes. For example, of the 10 lakes that had changed significantly since preindustrial times, 90% had acidified. All of the lakes with measured pH < 6, and 63% of lakes with a pH < 6.5, showed a decline in pH (Fig. 2*c*). In contrast, 71% of lakes with a measured pH > 7 increased in pH, although only one lake had increased significantly since preindustrial times (Fig. 2*c*). Equal numbers of circumneutral lakes (measured pH 6.5–7) either increased or decreased in pH (Fig. 2*c*).

Top–bottom paleolimnological studies, using scaled chrysophytes as indicators of environmental change, have reported similar trends in Sudbury, Ont. (Dixit et al. 1992*b*) and the Adirondacks (Cumming et al. 1992*b*). However, the magnitude of change was considerably smaller in south-central Ontario, with only one lake showing acidification of greater than 1 pH unit. In part, this discrepancy may reflect the gradient of lakes examined in the Muskoka study. Very acidic lakes (i.e., measured pH < 5.5), which often show the greatest declines with acid deposition (e.g., Cumming et al. 1992*b*; Dixit et al. 1992*b*), were excluded from this data set, thereby underestimating the extent of overall acidification in this region. Furthermore, inferred values of preindustrial pH were higher in the Muskoka than the Adirondack lakes, suggesting that the former were comparatively well buffered, and therefore more resistant to acidification (Cumming et al. 1994). Finally, the amount of sulphate deposition, as measured in the early 1980s, has been considerably less in south-central Ontario (LaZerte and Dillon 1984, 70–100 $\mu eq \cdot L^{-1}$) than in the Sudbury region (Keller et al. 1992, >200 $\mu eq \cdot L^{-1}$), which may have contributed to the smaller inferred changes in the Muskoka lakes (Smol et al. 1998).

Diatom (Hall and Smol 1996), chrysophyte cyst (Wilkinson et al. 1999), and scaled chrysophyte (this study) inference models suggest that study lakes with a measured pH > 7 have increased in alkalinity since preindustrial times. In south-central Ontario and in other regions receiving elevated acidic deposition (e.g., Sudbury, Dixit et al. 1992*b*; Adirondacks, Cumming et al. 1992*b*), several mechanisms may have contributed to the observed increases in alkalinity. First, the disturbance or removal of watershed vegetation may increase soil erosion, causing an increase in the export of base cations (e.g., Rhodes and Davis 1995). The removal of forests for timber in the late 1800s, the building of roads, and the construction of seasonal cottages and resorts are dis-

Fig. 7. Scatter-plots of predicted and measured pH from 48 lakes in south-central Ontario, calculated using (*a*) diatom (Hall and Smol 1996), scaled chrysophyte, and chrysophyte cyst (Wilkinson et al. 1999) inference models, and (*b*) combined inferences weighted by the r^2 and root mean squared error (RMSE) of the individual inference models.



turbances that may have contributed to this process. The importance of these disturbances on the acid–base chemistry of the lakes will be regulated by watershed characteristics (e.g., underlying geology, drainage ratio, catchment slope). For example, greater than 85% of the lakes that increased in alkalinity overlie a marble intrusion and are relatively well buffered compared with lakes situated on granitic bedrock (Wilkinson et al. 1999) (Fig. 2*c*).

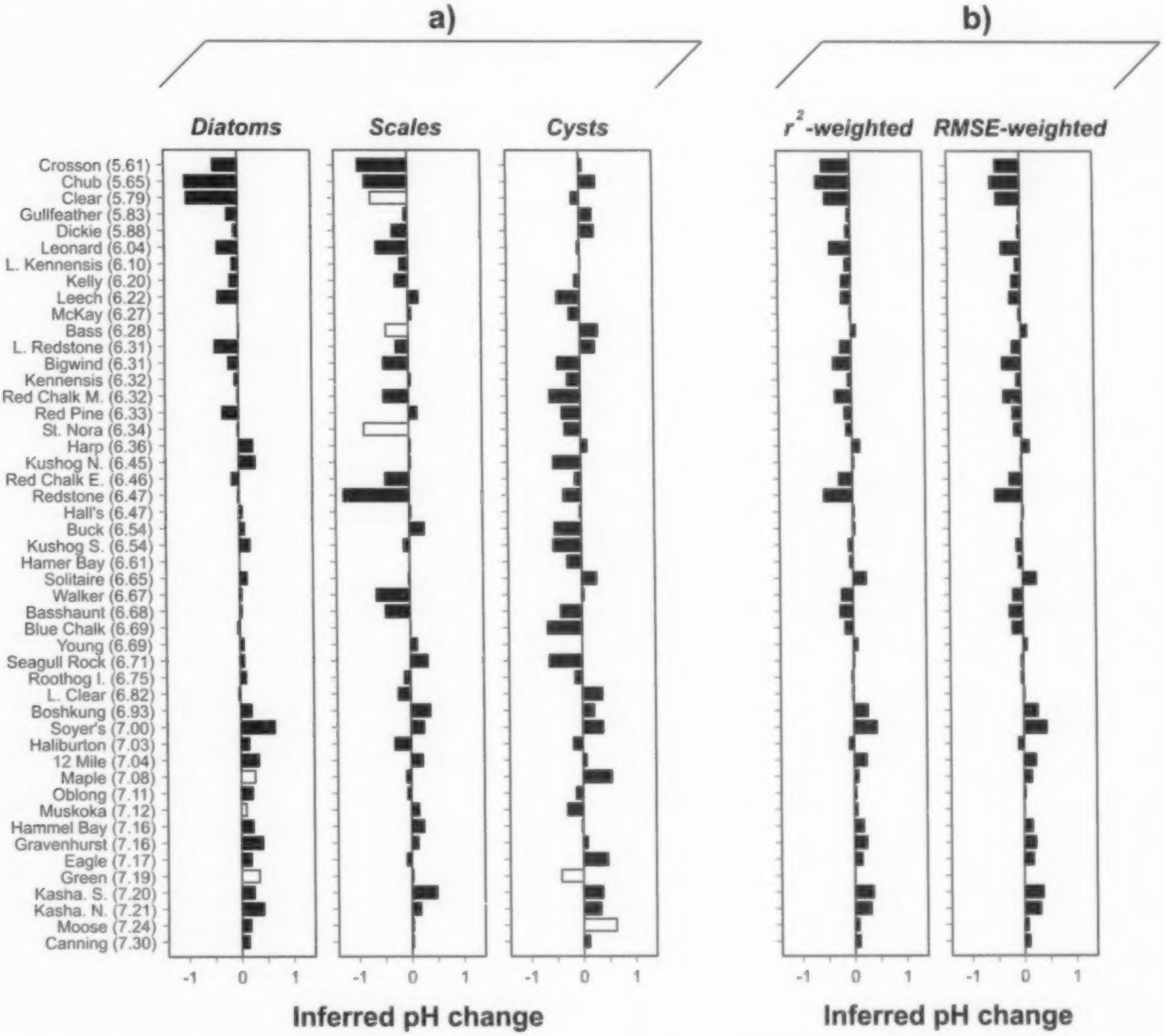
Cation exchange and sulphate and nitrate reduction in watershed soils, wetlands, and lake sediments are other processes that may have contributed to the observed increases in alkalinity in the Ontario lakes (e.g., Dillon et al. 1997). These too are regulated by watershed characteristics (e.g., percent wetlands) and by changes in climate, which may cause a reversal of these trends immediately following drought (Yan et al. 1996). Without knowing the timing of changes in these lakes, we cannot separate the contributions of these mechanisms into those attributable to alkalinity generation. Analyses of continuous sediment cores will be required to further address these questions.

A multiple-indicator measure of lake acidification in the Muskoka–Haliburton region

At a regional scale, pH inferences from the diatom and chrysophyte models showed similar trends, with greater than 60% of the lakes indicating a nonsignificant change since preindustrial times. These similarities were not always apparent at a lake scale. Scaled chrysophyte and diatom models showed moderate agreement ($r = 0.56$, $n = 48$, $p < 0.001$) across lakes in inferring changes in lakewater pH. In general, scaled chrysophytes inferred a greater decrease in pH, which may reflect organism-specific differences in habitat and life history (see below). Inferences derived from chrysophyte cysts showed little agreement with the scaled chrysophyte ($r = 0.00$, $n = 48$, $p > 0.05$) or diatom models, which may reflect differences in the predictive ability of the inference models (Fig. 7). Although chrysophyte cysts have been shown to be sensitive indicators of lake acidification (Smol 1995), cyst models generally do not perform as well as diatom or scaled chrysophyte models developed with comparable data sets. This may reflect variation associated with cyst taxonomy and identification. Furthermore, cysts represent a resting stage, and therefore abundances may not directly reflect conditions in the planktonic environment.

The existence of three models for inferring lakewater pH in the Muskoka region introduces an interesting dilemma for lake managers. Whereas each model may provide unique ecological information, a question arises as to which environmental reconstruction to believe. One option is to take a conservative approach and to base management decisions on the paleolimnological indicator that is inferring the greatest amount of change since preindustrial times. However, this approach does not consider differences in the predictive ability of the individual inference models, and may also result in

Fig. 8. The inferred pH change of 48 lakes in south-central Ontario, calculated using (*a*) diatom (Hall and Smol 1996), scaled chrysophyte (Paterson et al. 2002), and chrysophyte cyst (Wilkinson et al. 1999) inference models, and (*b*) combined models weighted by r^2 or root mean squared error (RMSE) of the individual models. Lakes are arranged in order of increasing measured pH. Open bars represent lakes in which fossil samples have poor modern analogs.



a loss of important ecological information. We propose an alternative approach that takes into account the predictive ability of each inference model, without sacrificing the ecological relationships of each indicator with its environment.

The combined reconstruction models, whether based on r^2-weighted or RMSE-weighted mean values, performed better than the models from individual indicators when used to predict the measured pH of the modern samples (Figs. 7*a* and 7*b*). There are at least two explanations for these trends. First, the combined models are calculated as averages of the indicator models, and therefore numerically smooth the biases associated with the individual models. For example, inference models from diatom and chrysophyte cysts underestimate and overestimate the measured pH of samples with a pH < 6 (Fig. 7*a*). Combining these inferences into a single prediction may have reduced the organism-specific biases, which are often greatest at the ends of the measured environmental gradient, resulting in an inferred value close to the measured pH.

Second, when reconstructions from several indicators are combined, the biological record is smoothed, and may more appropriately match the resolution of the environmental data. In our training set, measured pH was calculated as an average of ice-free measurements over the 1990–1992 seasons. Similarly, the biological data of each indicator was smoothed temporally, representing the top 1 cm of each sediment core (approximately 2–5 years in this region). However, the deposition of each indicator is not constant through the ice-free season. For example, several chrysophyte taxa reach population maxima immediately after ice-out, with smaller maxima in the fall (Sandgren 1988). The contribution of chrysophyte scales and cysts to the lake sediment may be dominated by seasonal periods of higher deposition. Therefore, combining the inferences of chrysophytes and diatoms may produce biological data that are more representative of the entire ice-free season, and reduce the impact of these seasonal biases. This is particularly important for environmental variables such as pH, which vary during the ice-free season. Snow-melt in early spring may contribute acidic run-off to Ontario lakes, resulting in a significant decrease in pH at this time (Smol et al. 1998). This may also explain why chrysophyte models generally show a greater acidification trend than the diatom model in south-central Ontario (Hall and Smol 1996; Wilkinson et al. 1999; this study) and in other regions (e.g., Cumming et al. 1992*b*; Dixit et al. 1992*a*).

Apart from the obvious increase in counting effort, the main disadvantage of combining inference models to infer lakewater pH is that the calculation of a mean reduces the impact of extreme values associated with each indicator, resulting in a smaller estimate of change since preindustrial times (Fig. 8). However, despite this smoothing trend, the mean pH change was comparable across lakes, regardless of the model used (mean pH change: diatoms, 0.01; chrysophyte scales, –0.14; cysts, –0.05; r^2-weighted model: –0.05 pH units; RMSE-weighted model: –0.05 pH units). Furthermore, if the smoothed biological data are a more reliable fit with the environmental data, as suggested above, then the smaller inferred changes may reflect true changes in these lakes. The combined models can only estimate environmental change at a resolution equal to that of the training set. Therefore, inferred changes in this study reflect mean conditions over three ice-free seasons. This combined inference approach may not be advantageous in other studies, where water chemistry data are representative of single measures or seasonal values.

Multiple indicators in paleolimnological studies are useful in that they may provide information about environmental change at an ecosystem level. However, because of differences in the predictive power of individual reconstruction models, prediction and random errors, and differences in the ecological preferences of organisms, the magnitude and direction of change inferred may vary across indicators. From a lake management perspective, interpreting these differences may be difficult. We have explored the use of a single, mean inference from three phycological indicators, which is weighted by either the coefficient of determination of the reconstruction models, or the prediction error. The combined models perform as well or better than the individual models when used to predict the pH of modern samples, suggesting that they can be used to infer the pH of lakes in south-central Ontario. Although inferences made using the combined models are smaller relative to the organism-specific models, they may be a truer reflection of the pH changes that have occurred in these lakes.

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Impact of lobster size on selectivity of traps for southern rock lobster (*Jasus edwardsii*)

S.D. Frusher and J.M. Hoenig

Abstract: Most lobster fisheries are characterized by high exploitation rates. This has led to substantial declines in the size structures of the populations over time as larger lobsters have been removed. Although both scientists and fishers have suggested that size related hierarchies could impact on lobsters entering traps, the effect of the size change on the selectivity of lobster traps as a population's size structure changes has not been investigated. This paper demonstrates that larger lobsters affect the entrapment of smaller lobsters and that this behaviour affects the selectivity of lobster traps. Both spatial and temporal (within season) factors were found to affect the selectivity plots. Spatial differences in selectivity were attributed to the broader size range of larger lobsters found in regions of faster growth. Temporal differences were attributed to the decline in larger lobsters over the course of a season caused by exploitation. There are also differences in trap selectivity between the sexes.

Résumé : La plupart des pêches commerciales de Homards ont des taux d'exploitation élevés, ce qui entraîne des déclins importants dans la structure en taille des populations dans le temps, à mesure que les plus grands homards sont retirés. Bien que les scientifiques aussi bien que les pêcheurs aient suggéré que les hiérarchies reliées à la taille pouvaient affecter l'entrée des homards dans les casiers, l'effet du changement de taille sur la sélectivité des casiers à homards, lorsque la structure en taille de la population se modifie, n'a jamais été étudié. Nous démontrons que la présence de plus grands homards affecte la capture des homards plus petits et que ce comportement modifie la sélectivité des casiers. Les courbes de sélectivité sont affectées à la fois par des facteurs spatiaux et des facteurs temporels (intra-saisonniers). Les différences spatiales sont attribuables à l'éventail plus étendu de tailles des plus grands homards dans les régions de croissance rapide. Les différences temporelles s'expliquent par la diminution du nombre de grands homards au cours de la saison à cause de l'exploitation. Il y a aussi des différences de sélectivité des casiers entre les sexes.

[Traduit par la Rédaction]

Introduction

Selectivity is a measure of the catchability of one component of a population (e.g., size class) relative to other components of the population for those animals that encounter a given type of fishing gear. Length-based estimates of fishing-gear selectivity are crucial in fisheries science if population parameters are to be estimated from length-structured catch data. Although selectivity of a variety of fishing gears has been estimated, recent papers have demonstrated that selectivity for a particular gear can change both spatially (Anganuzzi et al. 1994; Addison and Lovewell 1991) and temporally (Myers and Hoenig 1997).

Over the last 30 years, the Tasmanian rock lobster (*Jasus edwardsii*) fishery has sustained a substantial decline in the biomass of legal-sized animals to a level of approximately 6% of an unharvested population (Frusher 1997). This has resulted in substantial changes to the size structure of the population, with the bulk of the legal-sized biomass being recently recruited lobsters. Larger lobsters are becoming increasingly rare in the catch (Frusher 1997).

In addition to having a legal-sized biomass based primarily on recruits, the Tasmanian rock lobster fishery has high exploitation rates in most regions (Frusher et al. 1998; Frusher and Hoenig 2001). Within a fishing season there is a substantial shift in the size structure of the population from large (recruited) lobsters to small (undersized) lobsters as large lobsters are harvested.

Most comparisons of the size composition of a population over both spatial and temporal scales assume that selectivity is constant and that the size distributions can be compared directly. Assessment techniques that compare size classes such as the change-in-ratio technique (Pollock and Hoenig 1998; Frusher et al. 1997, 1998) also assume that the selectivity of the size classes being considered does not change between surveys.

Although it is recognized that behavioural changes like those associated with molting affect catchability of lobsters (Morgan 1974; Newman and Pollock 1974; Krouse 1989), behaviour also affects selectivity, as Frusher et al. (1998) found larger lobsters to molt earlier during their molting period. Another factor that could affect selectivity may be the

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presence of size-related dominance hierarchies. Olsen (1958) and Winstanley (1977) suggest that dominant larger-sized lobsters could prevent smaller lobsters from entering traps. Addison (1995) and Miller (1979, 1990) suggest that fishing pressure would remove these dominant lobsters and thus influence the size distribution of lobsters entering a trap during the fishing season.

Larger lobsters have been found to have higher catchabilities than smaller lobsters and males to be more "catchable" than females (Miller 1989). Different styles of traps and different areas have also been found to produce different trap selectivity (Addison and Lovewell 1991). However, there have been no studies on the impact on trap selectivity associated with harvest of a population over time.

This paper uses tagging data collected from fishery-independent catch sampling surveys undertaken from 1992 to 1998 to evaluate temporal and spatial changes in selectivity of rock lobsters in research traps around Tasmania. Tagging data were also obtained from a study of an unfished population in a marine reserve.

Materials and methods

Reserve sampling

Site, procedure, and sampling gear

The Crayfish Point Reserve was established in 1971 and is located in the Derwent estuary in Tasmania (Fig. 1). The reserve extends 800 m from the shoreline and covers an area of 1.0 km^2. Habitat maps of the reserve indicate that approximately 40% of the reserve is lobster habitat. In 1999, two surveys were undertaken from 28 January to 18 February and from 30 March to 10 April. During each survey, 50 baited lobster research traps were set each day and hauled approximately 24 h later during the following morning. Traps were set randomly on the lobster habitat and each region of lobster habitat was sampled at least once during each survey. All lobsters caught in each trap were measured to the nearest millimetre of carapace length (CL) and sexed. All lobsters were transported to an adjacent shore-based holding facility at the Tasmanian Aquaculture and Fisheries Institute's marine laboratories. Lobsters greater than 80 mm CL were tagged ventrally in the flesh of the first abdominal segment (Hallprint T-bar anchor tag; TBA1, Hallprint Pty. Ltd., 27 Jacobsen Crescent, Holden Hill, South Australia 5088, Australia). All lobsters were released back into the reserve at the completion of each survey.

Research traps were similar to the square steel traps that are becoming increasingly popular in southern parts of the fishery and are described in Frusher et al. (1998). The main difference between research traps and commercial traps was that research traps had no escape gaps, which are mandatory for commercial fishing operations. The escape gaps are to allow undersized lobsters to escape without having to be handled during the fishing operation.

Investigating the potential interaction between different sizes in traps

To investigate whether small lobster catchability was influenced by the presence of larger lobsters, three analyses were undertaken for the reserve data. (*i*) Catch rates (number of lobsters per trap lift) of small (<90 mm CL) and large lobsters (>140 mm CL) were compared for each day of both surveys. (*ii*) Correlations between the number of small (<90 mm CL) and large (>109 mm CL) lobsters caught in each trap of both surveys were undertaken. Large lobsters were defined as being greater than 109 mm CL for this analysis so that the results could be compared with the regional fishing ground data. Southern regions had no lobsters in the >140 mm CL category. (*iii*) Selectivity curves based on recaptures of tagged lobsters caught during the first four days and last four days of the second survey were compared.

There were no other reserve areas available to determine if there are any changes in catch rates when lobsters are not removed. However, lobster sampling was identical in surveys undertaken in the reserve in January and December 2000, with the exception that lobsters were released immediately after being measured, sexed, and tagged. We use these surveys to check on the possibility of temporal changes in catch rate occurring independently of removals. Because the data are not bivariate normally distributed, we used Spearman's rank correlation coefficient to test for significance of association.

Estimating selectivity

Recaptures in the second survey of lobsters tagged in the first survey were used to estimate selectivity. Selectivity could only be determined for male lobsters as female lobsters began to molt between surveys (P. Zeigler, Tasmania Aquaculture and Fisheries Institute, personal communication).

Selectivity (ϕ_l) was determined for each 10 mm CL size class by the proportion of tags returned in the second survey from tagging in the first survey

$$(1) \qquad \phi_l = \frac{(N_{Rl}/N_{Tl})}{\max_l(N_{Rl}/N_{Tl})}$$

where N_{Tl} is the number of lobsters tagged in size class l during the first survey and N_{Rl} is the number of lobsters of size class l tagged in survey 1 that were recaptured in survey 2. The denominator serves to standardize the selectivity estimates to the interval (0,1). Selectivity was not calculated for size classes where fewer than 20 lobsters were tagged in the first survey.

Research sampling on the fishing grounds

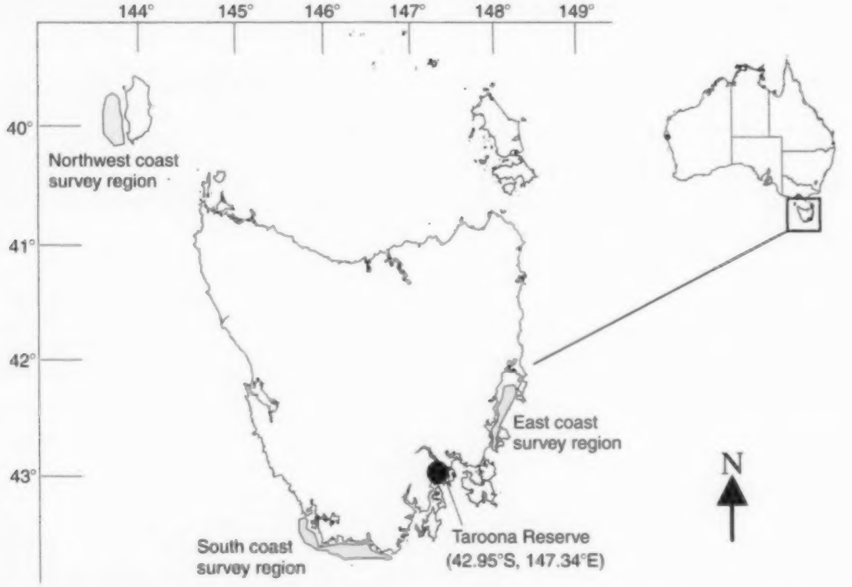
Sites, procedure, and sampling gear

Three regions in Tasmania were used to investigate the interaction between different sizes of lobsters caught in traps (Fig. 1). These regions span a range of growth rates from slow growth in the southern region to fast growth in the northern region (Frusher 1997). Only the southern and eastern regions that were sampled from 1992 to 1998 in a fishery-independent catch sampling project were used to determine selectivity in fished regions (Fig. 1). Selectivity could not be determined in the northwestern region because sites were not resampled during each survey and thus there were no recaptures suitable for determining selectivity.

The Tasmanian fishing season opens in November and closes at the end of April and August in the following year for female and male lobsters, respectively. Surveys were undertaken three times each year. A preseason survey was undertaken in October–November, a second survey was conducted in March prior to the female molt (April to May), and the final survey was conducted in July–August prior to the male molt (September to October) (Frusher et al. 1998). On the south and east coasts there are 4 sampling sites and, if weather allowed, we attempted to sample each site twice during each survey. Traps are set randomly within each site, although the sizes of the sites are relatively small (<0.5 km^2), thus the majority of lobster habitat is sampled each survey. Each survey consisted of eight and nine overnight fishing shots in the eastern and southern regions, respectively. Each shot involved the setting of 50 identical research lobster traps. Tagging was conducted during each survey. To ensure that the collected data represented the catch from the commercial fishery, sites were selected after consultation with fishers.

Sampling gear was the same as that used in the reserve. From each trap, all lobsters were measured and sexed and in regions where catch rates of lobsters were high, tagging was restricted to

Fig. 1. Map of Tasmania, Australia, showing the southern, eastern, and northwestern regions surveyed and the location of the Crayfish Point (Taroona) Reserve.


144°
145°
146°
147°
148°
149°
40°
41°
42°
43°
Northwest coast survey region
East coast survey region
South coast survey region
Taroona Reserve (42.95°S, 147.34°E)
N

approximately 1000 lobsters per survey This was achieved by tagging the first 200 lobsters per shot. All lobsters (newly tagged, recaptures, and untagged) were released back in their site of capture. Tagging surveys were used to determine selectivity when the difference in the mean of tagged and recaptured lobsters differed by less than 5 mm CL and 4 mm CL on the east and south coasts, respectively.

Investigating the potential interaction between different sizes in traps

To investigate whether there was an interaction between the catchability of small and large lobsters, the correlation was estimated for the number of small lobsters (<90 mm CL) and large lobsters (>109 mm CL) caught in individual research traps. As for the reserve data, Spearman's rank correlation coefficient was used to test for significance of association.

Estimating selectivity

On the commercial fishing grounds, selectivity estimates could only be made from surveys where recaptures were obtained from lobsters tagged during each specific survey (e.g., only recaptures obtained during the March 1994 survey from lobsters tagged during the March 1994 survey could be used). Both molting and harvesting of legal-sized lobsters affected the size distribution of tagged lobsters between surveys.

Selectivity (ϕ_{li}) was determined for each 5 mm CL size class by the proportion of tags returned on subsequent days after tagging during each survey

$$(2) \qquad \phi_{li} = \frac{(N_{\mathrm{R}li}/N_{\mathrm{T}li})}{\max_{li}(N_{\mathrm{R}li}/N_{\mathrm{T}li})}$$

where $N_{\mathrm{T}li}$ is the number of tagged lobsters for each size class l during survey i and is derived from

$$(3) \qquad N_{\mathrm{T}li} = \sum_{j=1}^{J-1} T_{lj}$$

where T_{lj} is the number of lobsters of length l tagged on day j of survey i, and J is the number of days in the survey. $N_{\mathrm{R}li}$ is the number of recaptured lobsters for each size class l during survey i and is represented by

$$(4) \qquad N_{\mathrm{R}li} = \sum_{j=2}^{J} R_{lj}$$

where R_{lj} is the number of lobsters of length l recaptured on day j of survey i.

Selectivity was not estimated for size classes where fewer than 20 lobsters were tagged. Multiple recaptures (the same lobster being caught more than once before the end of a sampling trip) were few and classified as a single recapture to minimize "trap happy" behaviour.

The principal aims of the tagging component of the fishery independent study were to obtain growth and movement information and molt frequency to aid in elucidating exploitation rate estimates in the fishery. Unfortunately there was insufficient data to evaluate seasonal selectivity for each year and thus it was necessary to combine all tagging events from the same survey time period (e.g., March) over all years.

On several occasions tagging focused on specific size groups. To estimate selectivity, tagging needs to be random or needs to target the same size classes over all surveys to be summed. To determine if a tagging event could be used in the selectivity study, the mean length of all lobsters caught was compared to the mean length of all lobsters tagged. Selectivity was determined for each sex separately.

Results and discussion

Interaction between different sizes in traps

Reserve

A significant negative correlation was found between catches of large and small lobsters in the reserve (Table 1). The correlations indicate that there is a sex effect, as large females have a higher negative correlation with both small females and small males than large males have with either small females or small males. This is despite males reaching larger sizes than females.

To further explore the impact of large lobsters on catchability of small lobsters, the daily catch rates of small and large lobsters during the reserve surveys were compared (Figs. 2*a* and 2*b*). Large lobsters showed a decline in catch rates as both surveys progressed, whereas small lobsters showed a gradual increase before beginning to decline. This suggests that the presence of large lobsters in traps at the beginning of the survey was preventing small lobsters from entering the traps. As the number of large lobsters decreased owing to their removal from the reserve, the catch rates of small lobsters increased until their numbers started to decline because of depletion from sampling activities.

To determine if the patterns over time of catch by size group might be due to temporal processes occurring independently of removals, we examined the catch composition over time when animals were trapped but immediately returned to the water (Fig. 3). The composition of the catch remained constant over time. This suggests that it is the reduced abundance of large lobsters that causes the catch rate of small lobsters to increase.

Fishing grounds

A significant negative correlation was also found between the number of small and large lobsters (regardless of sex) caught in traps during surveys of the Tasmanian rock lobster fishing grounds in each of the three regions surveyed (Table 1). With the exception of the correlation between large males and small females on the south coast, all negative correlations increase from southern to northern Tasmania, as does the size range of lobsters caught (Fig. 4). The reason for the high negative correlation for large males and small females in the south is unknown. The trend in the other correlations would suggest a size-related dominance hierarchy. Agonistic interactions between different-sized *Homarus americanus* have been reported by Schrivener (1971), Miller (1995), and Karnofsky and Price (1989).

Similar to the situation in the reserve, large females from eastern Tasmania had a higher negative correlation with small lobsters of either sex than large males had with small lobsters of either sex. Both the correlations from the three regions of Tasmania and the catch rates obtained from the reserve suggest that the presence of larger lobsters affects the entrapment of smaller lobsters.

Selectivity

To use tag recapture information to determine selectivity, we assume that the number of tagged lobsters within each length class in the survey area at the time of recapture is directly proportional to the number of tagged lobsters within the same size class that were released during the first survey. Size-dependent effects such as molting, emigration, natural mortality, tag loss, or tag-induced mortality would bias selectivity estimates. Molting between surveys was only found to occur for females in the reserve and female selectivity plots for these data have not been attempted. Pearn (1994) found virtually no migrations of lobsters in southern and eastern Tasmania, Treble (1996) found tag loss to be around 1% for *J. edwardsii* in southern Australia and Kennedy (1992) estimated natural mortality to be $0.1\cdot\text{year}^{-1}$. We found a combination of tag loss, tag-induced mortality, and tag reporting rate to be $0.23\cdot\text{year}^{-1}$ in northwestern Tasmania (Frusher and Hoenig 2001). The magnitudes of these effects appear to be low over the study period. Thus, it does not appear likely that these effects can vary greatly by size class.

Table 1. Correlation results between small (S, <90 mm carapace length (CL)) and large (L, >109 mm CL) male (M) and female (F) lobsters caught in the southern, eastern, and northern regions of the fishery from 1992 to 1998 and in a reserve in southeastern Tasmania in 1999 (Fig. 1).

Region		LM:SM	LM:SF	LF:SM	LF:SF
Southern					
	Correlation	–0.1227	–0.3426	–0.0885	–0.0379
	P value	0	0	0	0.0165
	N	4903	5179	4178	3997
Eastern					
	Correlation	–0.3767	–0.2596	–0.4560	–0.3489
	P value	0	0.0001	0	0
	N	3111	3496	2561	3083
Northern					
	Correlation	–0.5265	–0.5290	–0.6621	–0.6586
	P value	0	0	0	0
	N	4904	5180	4179	3998
Reserve					
	Correlation	–0.2850	–0.3211	–0.3983	–0.4065
	P value	0	0	0	0
	N	923	944	588	607

Note: Spearman's rank correlation coefficients are presented followed by their *P* values. *N* is the number of pairs used in each correlation.

Reserve

The male selectivity plot for recaptures obtained in survey 2 from lobsters tagged in survey 1 shows a linear increase with size up to 170 mm CL (Fig. 5*a*). To determine the effect of a size interaction on selectivity, selectivity was estimated for the first and last four days of the second survey period (Fig. 5*b*). The start of the survey showed a gradual increase in the selectivity plot up to 145 mm CL, which was followed by a sharp rise to a peak selectivity of very large (170 to 180 mm CL) lobsters. In contrast, the selectivity plot for the latter four days of the survey had increased selectivity of smaller lobsters (<120 mm CL) and peak selectivity in the 140 to 170 mm CL range.

Fishing grounds

Male lobsters caught during surveys on the east coast of Tasmania show an increase in selectivity with size, peaking at the size grouping above the legal size limit of 110 mm CL by 5 mm CL (Fig. 6*a*).

The slope of the selectivity plot for the start of the fishing season is less than the middle- and end-of-season plots. At the middle and end of the fishing season there is an increased selectivity for lobsters in the size range from 80 mm CL to 110 mm CL relative to the selectivity at the beginning of the season. The similarity between the middle- and end-of-season selectivity plots would be expected, as over 80%

Fig. 2. Comparison of catch rates in the reserve for small (<90 mm carapace length (CL), open circles) and large (>140 mm CL, solid circles) lobsters in (*a*) survey 1 and (*b*) survey 2. The polynomial equations describe the catch rate (CR) as a function of the day (t) of the survey. For survey 1, the equations are $CR = -0.0012t^2 - 0.0019t + 0.6716$ ($R^2 = 0.4303$) for large lobsters and $CR = -0.0028t^2 - 0.058t + 0.0701$ ($R^2 = 0.3531$) for small lobsters. For survey 2, the equations are $CR = -0.0007t^2 - 0.0383t + 0.6757$ ($R^2 = 0.6985$) for large lobsters and $CR = -0.0089t^2 - 0.0844t + 0.0096$ ($R^2 = 0.3357$) for small lobsters.

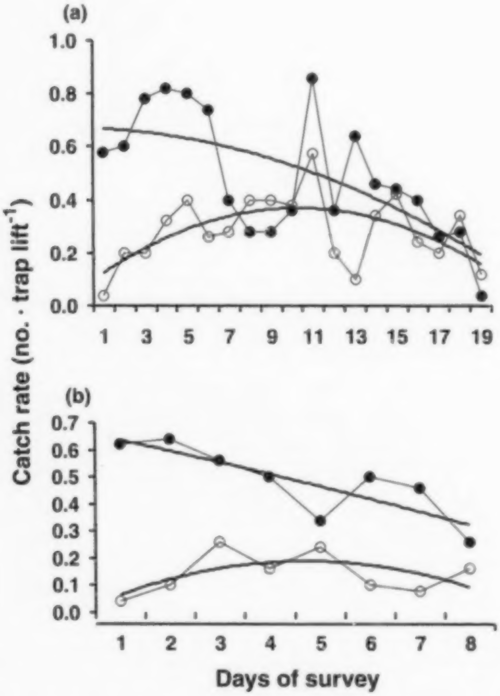


Fig. 3. Proportion of legal-sized male lobsters caught during each day of three surveys undertaken in January 1999 (solid circles) and 2000 (open circles) and December 2000 (open squares). In January 1999, lobsters were removed from the survey site during the period of the survey. In January and December 2000, lobsters were released into the survey site immediately after capture.

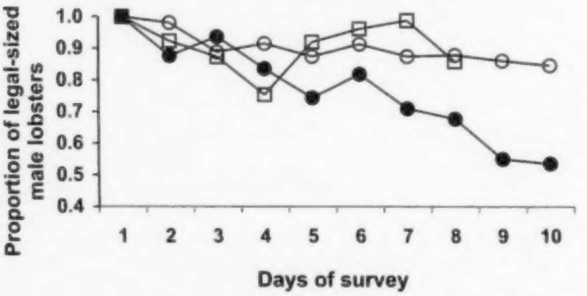


Fig. 4. Regional size structure of male lobsters from northern (solid circles), eastern (open circles), and southern (solid squares) Tasmania.

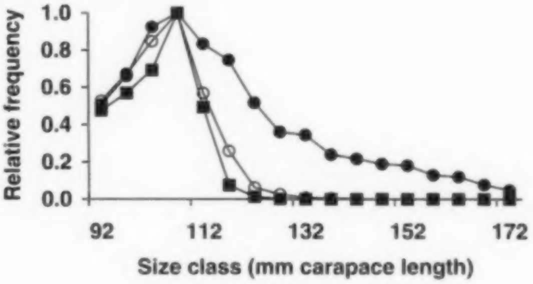
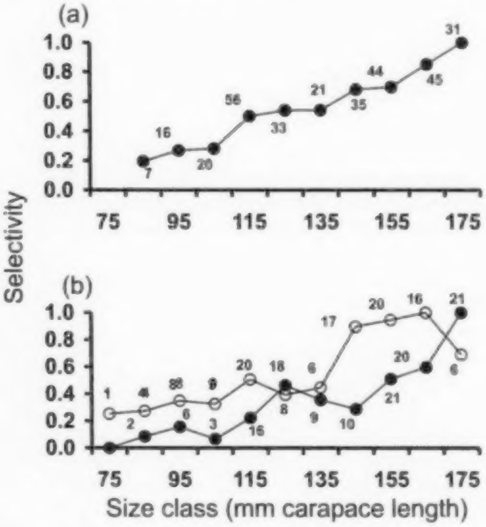


Fig. 5. Estimated selectivity for male lobsters in the reserve for (*a*) the entire second survey and (*b*) the first 5 days (solid circles) and last 5 days (open circles) of the second survey. Numbers refer to numbers of recaptures.



of the commercial catch on the east coast has been taken by the middle survey period (Frusher et al. 1998). This is reflected in the size structure of the population that shows a decline in the legal-sized lobsters between the start and middle season and limited change between the middle and end of season (Fig. 7*a*).

For female lobsters on the east coast, the difference in selectivity plots within a season is less pronounced (Fig. 6*b*). The start and end-of-season selectivity plots both peak at the 90 to 100 mm CL interval and are similar in shape except for the 70 to 80 mm CL interval. The small number of lobsters tagged in this size interval possibly accounts for this discrepancy. The similarity between the plots at the start and end of the fishing season is expected because the commercial season for female lobsters closes after the middle season survey. After this survey, female lobsters molt and thus all legal-sized lobsters for the forthcoming seasons are available for capture during the end-of-season survey. Although the size structures of legal-sized female lobsters at the start and end of the fishing season are not identical (Fig. 7*b*), they are less different in shape compared to the middle-season size structure.

Fig. 6. Estimated selectivity for (*a*) male lobsters from the east coast of Tasmania, (*b*) female lobsters from the east coast of Tasmania, and (*c*) male lobsters from the south coast of Tasmania at the start (solid circles), middle (open circles), and end (open squares) of the fishing season.

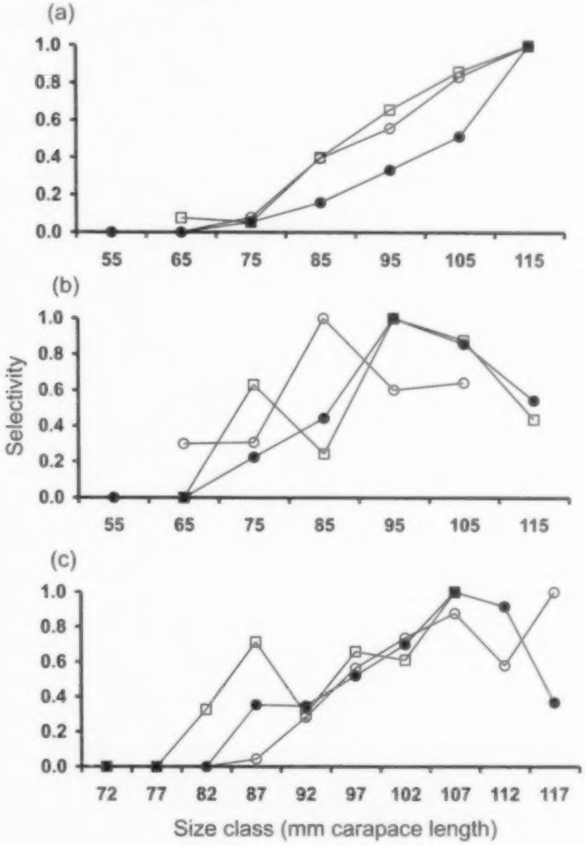
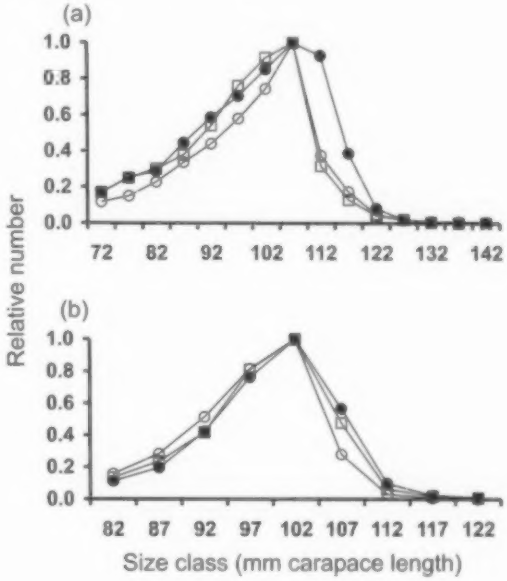


Fig 7. Relative size structure of (*a*) male lobsters caught in traps on the east coast and (*b*) female lobsters caught in traps on the east coast at the start (solid circles), middle (open circles), and end (open squares) of the fishing season.



The analysis for the south coast is restricted to males, as females represent less than 5% of the catch (Frusher 1997). There is very little difference between the selectivity plots for the three survey periods (Fig. 6*c*). Because of the slow growth and high exploitation in this region there are very few large lobsters. Less than 13% of the male catch comprised lobsters greater than 140 mm CL on the south coast, whereas over a third of male lobsters were above this size on the east coast.

Comparison between sexes

Selectivity of male and female lobsters was compared for the east coast, where there is a high probability of recapturing tagged lobsters of both sexes. To demonstrate the relative differences, the maximum fraction recovered from either sex was used to standardize both plots. In all survey periods, large males had the highest selectivity (Fig. 8). Selectivity for both sexes was similar for lengths up to approximately the 90 to 100 mm CL interval (start and end) and the 80 to 90 mm CL interval (middle). Above these intervals, female selectivity declined, whereas male selectivity continued to increase. This may be related to maturity of females, since the size at which 50% of females are mature on the east coast is just below the 80 to 90 mm CL interval (Frusher 1997). These results are similar to those reported by Miller (1995), who found the catchabilities of small male and female *H. americanus* to be similar but then to increase more rapidly for males.

Comparison between regions

Regional comparisons of selectivity can be made between males on the south and east coasts. In all periods within the fishing season, south coast and east coast male selectivity peaked at the size range below and above the legal size limit of 110 mm CL, respectively (Fig. 9). At the start of the fishing season, undersized males above 80 mm CL from the south have a higher selectivity than east coast males. As the season progresses, the trends in the selectivity plots become similar.

The correlation data (Table 1) suggested that large males (>109 mm CL) had a larger impact on small males on the east coast compared with the south coast. The regional difference between the selectivity plots at the start of the season is considered to be due to the large males impacting small males, and thus shifting the selectivity plot towards large lobsters. The similarity between the selectivity plots at the end of the season is expected, as the majority of legal-sized lobsters (≥110 mm CL) would be removed by exploitation from both regions.

In conclusion, the above results support fishers' beliefs that large lobsters exclude small lobsters from traps. The correlation data demonstrated that if a large lobster is in a trap it is unlikely that there will be many small lobsters and vice versa. This negative correlation was strongest in regions where large lobsters were abundant. The catch data from the

Fig. 8. Comparison of selectivity for male (solid circles) and female (open circles) lobsters on the east coast for the (*a*) start, (*b*) middle, and (*c*) end of the fishing season.

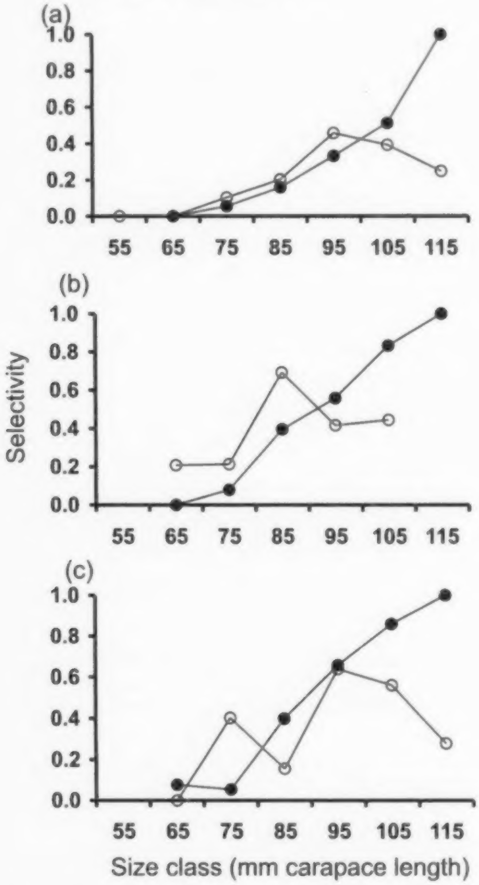
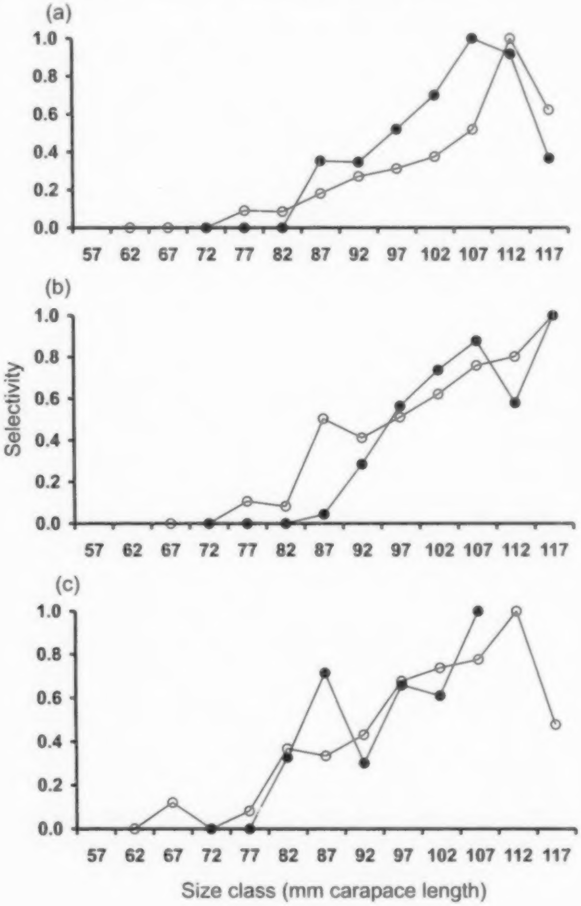


Fig. 9. Comparison of selectivity for male lobsters between the south (solid circles) and east (open circles) coasts for the (*a*) start, (*b*) middle, and (*c*) end of the fishing season.



reserve demonstrated that when large lobsters were present, they dominated the catches. As these large lobsters were removed, smaller lobsters became increasingly catchable. This behavioural interaction between small and large lobsters affects the selectivity of the traps. In regions where large lobsters are found, such as the east coast and the reserve in Tasmania, seasonal selectivity plots shift in favour of smaller lobsters as large lobsters are caught. In contrast, the selectivity plots for the southern Tasmanian region showed no differences between the start, middle, and end of season. This was supported by the very low correlation between large and small lobsters and is assumed to be due to the lack of large lobsters in this region. The lack of large lobsters is due to the high exploitation rates (Frusher et al. 1998) and the slow growth (Punt et al. 1997).

The slow growth in the south suggests that it is physical size rather than age that is causing the hierarchical dominance. Owing to their slower growth, lobsters around the minimum legal size limit of 110 mm CL would be substantially older in southern regions than in more northerly regions. The declining growth rate from northern to southern regions of Tasmania would also increase the age difference between small (<90 mm CL) and large (>109 mm CL) lobsters used in the correlation. This further supports the suggestion that it is size rather than an age-related dominance hierarchy.

Although various authors (see Miller 1989, 1995) have found catchability of larger lobsters to be greater than smaller lobsters and that large males have higher catchability than larger females, there has been no exploration of the impact of harvesting on selectivities. This paper demonstrates that selectivity can change with harvesting, even over small time frames such as within a fishing season. Assessment models for lobster fisheries, which use fixed selectivity plots, are likely to overestimate recruitment and this would be compounded over time as legal-sized biomass is fished down. Conversely, these models are likely to under-represent recruitment in fisheries, such as the Tasmanian rock lobster fishery, where management controls are aimed at rebuilding legal-sized biomass. We believe that the impact of varying selectivity on assessment of commercial lobster resources requires further investigation.

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Estimating natural and fishing mortality and tag reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear tagging model

S.D. Frusher and J.M. Hoenig

Abstract: Fishing and natural mortality rates and tag reporting rate for rock lobsters (*Jasus edwardsii*) in northwest Tasmania, Australia, were estimated using multiyear tagging models. These estimates are necessary for assessment of the resource. Several models were examined that had either two or three tagging events each year, and either combined sexes or kept sexes separate. The model that best described the dynamics of the fishery utilized three tagging events within a year. The year was divided into discrete periods and, within each year, fishing effort and duration of period were used to apportion fishing and natural mortalities, respectively, to the periods. The separation of fishing mortalities by sex was not found to improve the models. Although high ($1.0–1.2 \cdot \text{year}^{-1}$), the instantaneous fishing mortality estimates were comparable to estimates obtained from other methods and the relative standard errors were low. Reporting rate estimates were also precise and indicated a lack of participation by the fishing industry. Estimates of natural mortality were low ($0.00–0.02 \cdot \text{year}^{-1}$) but imprecise.

Résumé : Les taux de mortalité naturelle et de mortalité due à la pêche ainsi que les taux de signalisation des étiquettes chez la langouste *Jasus edwardsii* dans le nord-ouest de la Tasmanie en Australie ont pu être estimés à l'aide de modèles pluri-annuels de marquage. Ces estimations sont nécessaires pour l'évaluation de la ressource. Plusieurs modèles ont été examinés qui comportaient deux ou trois sessions de marquage chaque année et qui combinaient ou séparaient les sexes. Le modèle qui décrit le mieux la dynamique de cette pêche commerciale utilise trois sessions de marquage dans l'année. L'année est divisée en périodes distinctes et, au cours de chaque année, l'intensité de la pêche et la durée de la période servent à répartir la mortalité naturelle et la mortalité due à la pêche dans les périodes. La répartition des mortalités dues à la pêche entre les sexes n'améliore pas les modèles. Bien qu'élevées ($1,0–1,2 \cdot \text{année}^{-1}$), les estimations des taux instantanés de mortalité due à la pêche se comparent aux taux obtenus par d'autres méthodes et les erreurs types relatives sont peu importantes. Les taux de signalisation sont aussi précis et démontrent un manque de coopération de la part de l'industrie de la pêche. Les estimations de la mortalité naturelle sont basses ($0,00–0,002 \cdot \text{année}^{-1}$), mais imprécises.

[Traduit par la Rédaction]

Introduction

Exploitation rates of crustaceans have often been estimated by depletion methods (Delury 1947; Leslie and Davis 1939). Recently, exploitation rates in the Tasmanian rock lobster (*Jasus edwardsii*) fishery have been estimated by change-in-ratio and index-removal methods (Frusher et al. 1997, 1998). These methods measure the relative change in abundance or composition, respectively, of the harvestable population over time. Like depletion methods, they require the population to be closed to immigration, emigration, and recruitment (Pollock and Hoenig 1998; Hoenig and Pollock 1998). However, in many fisheries the population is not closed and the methods used to estimate exploitation rate must follow a specified portion of the resource over time.

Tagging studies on lobsters in northern Tasmania have shown that legal-sized lobsters close to the minimum size limit molt twice a year and there is a residual amount of molting occurring throughout the year. As the population is changing throughout the year, a change in legal-sized lobster abundance would relate to recruitment (molting from undersized to legal size) as well as fishing and natural mortality. Tagging studies mark and identify cohorts of animals, thus immigration and recruitment do not affect estimation of mortality rates. The effects of molting need to be eliminated so that a decline in legal-sized lobster abundance relates spe-

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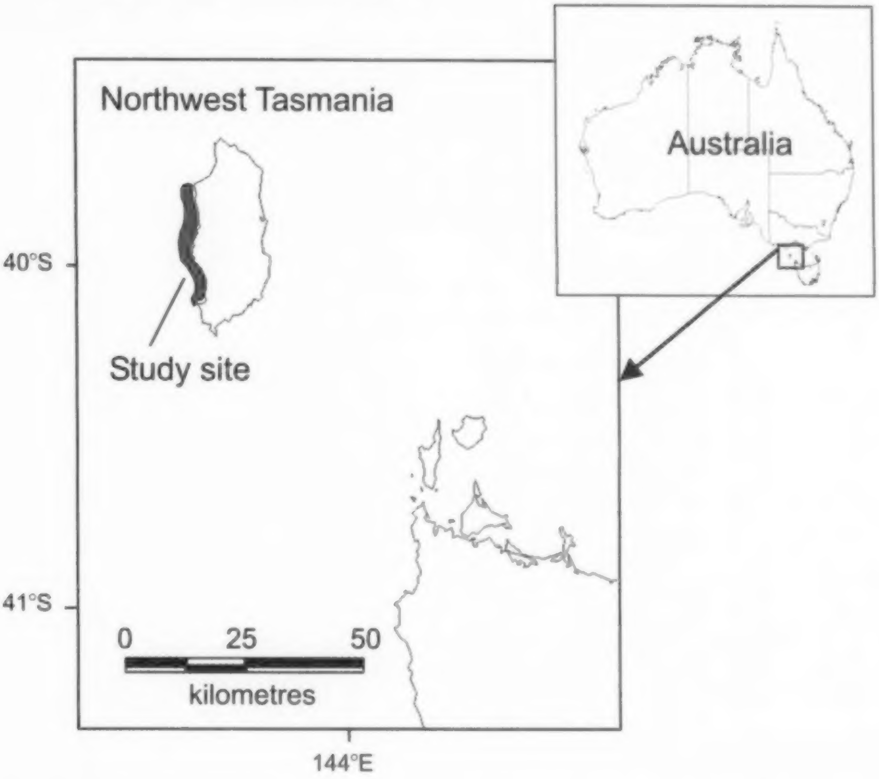
Fig. 1. Map of Australia showing northwest Tasmania and study site.



cifically to those lobsters that were present at the start of the fishery.

Tagging studies undertaken from 1992 to 1995 had the objective of obtaining growth and movement data. Despite this, we found that the data could be used to develop and evaluate tagging models for estimating mortality rates. This paper evaluates these models.

Brownie et al. (1985) presented a number of models for estimating year-specific survival and tag recovery rates from multiyear tagging studies. Kleiber et al. (1987) expressed tag return data in terms of tag reporting rate and fishing and natural mortality. Hoenig et al. (1998) reparameterized the multiyear tagging models of Brownie et al. (1985) in a very general formulation that expresses survival in terms of instantaneous rates of fishing and natural mortality. The recovery rate parameter was expressed as a product of three factors: the exploitation rate, tag reporting rate, and a parameter that includes tag loss and tag-induced mortality. The exploitation rate can be expressed as a function of the fishing and natural mortality rates. Tag loss and tag-induced mortality can be determined from separate studies, such as aquarium and double-tagging trials. Although tag reporting rate can theoretically be estimated from the models, Hoenig et al. (1998) found that tag reporting rate estimates were unreliable unless there are many years of tagging with a wide range of fishing mortality rates.

Hearn et al. (1998) described a model that used tagging data from tagging twice per year to estimate fishing and natural mortality. They were also able to estimate tag reporting rate. Their model has a fishing period where both fishing and natural mortality affect survival and a closed period of the year where only natural mortality affects survival. Tagging is undertaken before and after the fishing year. We combined aspects of the models described by Hearn et al. (1998) and Hoenig et al. (1998) to describe the dynamics of the lobster stock from the King Island area in northwest Tasmania.

Materials and methods

Study design

From 1992 to 1995, lobsters were tagged during research cruises off the coast of northwest Tasmania on the commercial fishing grounds (Fig. 1). The same tagging sites were visited on all cruises. Lobsters were tagged immediately upon capture and released at the site of capture. Lobsters were tagged with individually numbered T-bar tags (Hallprint T-bar anchor tag: TBA1, Hallprint Pty. Ltd., 27 Jacobsen Crescent, Holden Hill, South Australia 5088, Australia). Lobsters were tagged in February, May, and September from September 1992 to May 1995.

Tagging sites were situated within the main fishing grounds. Pearn (1994) found that legal-sized lobsters were primarily recaptured in the location of release. All of the available habitat for *J. edwardsii* is routinely fished each season.

Notices requesting return of tags were posted to all fishers and processors known to process Tasmanian rock lobsters. To encourage participation a tag lottery was established. Each correctly completed tag return represented an entry into the lottery. Advertising of the tagging project was undertaken by regular articles in the

Table 1. Annual proportion of time based on fishing effort (pot lifts) and time (days) used to calculate fishing and natural mortality.

Fishing season	Data						
1991–1992	Dates					11 May–31 Aug.	1 Sept.–19 Sept.
	Pot lifts (males)					0.17	0
	Pot lifts (females)					0	0
	Day					0.31	0.052
1992–1993	Dates	20 Sept.–31 Oct.	1 Nov.–6 Feb.	7 Feb.–31 Apr.	1 May–10 May	11 May–31 Aug.	1 Sept.–19 Sept.
	Pot lifts (males)	0	0.392	0.402	0.029	0.177	0
	Pot lifts (females)	0	0.494	0.506	0	0	0
	Day	0.115	0.271	0.225	0.027	0.31	0.052
1993–1994	Dates	20 Sept.–17 Nov.	18 Nov.–13 Feb.	14 Feb.–31 Apr.	1 May–10 May	11 May–31 Aug.	1 Sept.–19 Sept.
	Pot lifts (males)	0	0.379	0.366	0.026	0.228	0
	Pot lifts (females)	0	0.509	0.491	0	0	0
	Day	0.164	0.238	0.208	0.027	0.31	0.052
1994–1995	Dates	20 Sept.–17 Nov.	18 Nov.–29 Jan.	30 Jan.–31 Apr.	1 May–22 May	23 May–31 Aug.	1 Sept.–19 Sept.
	Pot lifts (males)	0	0.235	0.422	0.082	0.261	0
	Pot lifts (females)	0	0.358	0.642	0	0	0
	Day	0.164	0.197	0.249	0.06	0.277	0.052
1995–1996	Dates	20 Sept.–30 Nov.	1 Dec.–6 Feb.	7 Feb.–31 Apr.	1 May–10 May	11 May–31 Aug	1 Sept.–19 Sept.
	Pot lifts (males)	0	0.268	0.415	0.041	0.275	0
	Pot lifts (females)	0	0.392	0.608	0	0	0
	Day	0.197	0.189	0.227	0.027	0.309	0.052
1996–1997	Dates	20 Sept.–17 Nov.	18 Nov.–6 Feb.	7 Feb.–31 Apr.	1 May–10 May	11 May–31 Aug.	1 Sept.–19 Sept.
	Pot lifts (males)	0	0.308	0.318	0.023	0.351	0
	Pot lifts (females)	0	0.492	0.508	0	0	0
	Day	0.164	0.222	0.225	0.027	0.310	0.052

Table 2. Terminology used to describe models.

Model code	Description
2×	Two tagging events per year (September and May)
3×	Three tagging events per year (September, February, and May)
S	*F*s estimated for separate sexes
Ct	*F*s estimated for sexes combined based on lengths of time of fishing periods
Ce	*F*s estimated for sexes combined based on amount of fishing effort in each sex's fishing period
yA	*F*s estimated for each year of recaptures
yC	*F*s estimated for all years combined (constant *F*)

fishing industry magazine (*Fishing Today*) and by regular oral presentations at the Tasmanian Rock Lobster Fishermen's Association meetings.

The Tasmanian rock lobster fishery opens in November for both males and females, although the exact date has varied slightly over the years from 1992 to 1995. The female and male fishing periods close at the end of April and August, respectively, of the following year. Although female lobsters are caught from May to the end of the male fishing period in August, it is mandatory that they be returned to the sea. These female lobsters are rarely checked for tags and any that were reported have not been included in the analysis. During the recapture periods, there were no reports of tagged female lobsters that died because of the fishing activity (e.g., from predation by an octopus in the trap). For application of the Hearn et al. (1998) method, September was a preseason tagging event and May was a postseason tagging event for females. Models developed in this paper utilize data on both sexes and two or three tagging events.

Development of statistical models for tagging data

To model the tag returns within a year, we need to have the fishing and natural mortality rates reflect what happens in each period between tagging events. Hoenig et al. (1998) derived formulae where fishing and natural mortality are prorated against fishing effort and the length of time since tagging, respectively. These formulae and their adaptation to our data are presented in Appendix A.

Parameter estimability and methods for fitting models

There is no universally applicable method for determining estimability of parameters. However, for these models the estimability can easily be demonstrated using the method of moments (Appendix B).

In practice, the models are fitted by the method of maximum likelihood. The recoveries over time from each cohort of tagged animals constitute an observation from a multinomial distribution. The cohorts are considered independent. Thus, the likelihood for the data is a product of the multinomials.

Models were fitted using the program SURVIV (White 1983). Because of the large number of parameters to be estimated, tag reporting rate λ and natural mortality rate M were held constant over all years. Program SURVIV was developed to estimate survival rates and these estimates are constrained to be between 0 and 1. As the instantaneous mortality rates can be larger than 1, the fishing mortality parameters were transformed:

$$\hat{F} = -\ln \hat{T}$$

where $\hat{F}$ is the instantaneous fishing mortality estimate and $\hat{T}$ is the exponential of the negative of the fishing mortality estimate. Thus, we estimated T and then obtained the estimate of F from $\hat{T}$. By the invariance principle of maximum likelihood estimation, the resulting estimate of F is a maximum likelihood estimate.

Standard errors (SE) of the fishing mortalities were obtained from the SEs of the estimated T parameters by application of the delta method (Seber 1982). Thus,

$$\mathrm{SE}(\hat{F}) = \frac{\mathrm{SE}(\hat{T})}{\hat{T}}$$

Models tested

The available data allowed for the testing of 12 models. These models were based on two tagging strategies: tagging twice (2×, in September and May) or three times (3×, in September, February, and May) per year. For each of these strategies, models were established to determine fishing mortalities for each sex separately or for sexes combined. For the latter, fishing mortality for each sex was specified as being proportional to the length of the fishing period for that sex (the length of the fishing period for females being 60% as long as the fishing period for males.) Alternatively, fishing mortality was specified as being proportional to the amount of fishing effort in the open fishing period for each sex (Table 1). Combining sexes is considered appropriate, as both male and female lobsters are attracted to fishing pots. Fishers consider both sexes equally catchable with the exception of periods when either sex is molting.

Each of these models estimated fishing mortality annually. However, it is possible to constrain the fishing mortality to be constant over the years, and models were also evaluated with F held constant over time. Models were described using the descriptors in Table 2. For example, 2×–Ct–yA refers to the model based on two tagging events with fishing mortality estimated annually for sexes combined based on length of fishing period.

Model selection

Initial model selection was based on parsimony. Burnham and Anderson (1998) describe parsimony as the concept that a model should be as simple as possible with respect to the model structure and number of parameters. Following the procedures of Burnham and Anderson (1998), we used Akaike's information criterion (AIC) to formally select models. This strategy compares the improvement in fit of models with increased numbers of parameters to the most parsimonious model. Only models with a substantial improvement in fit are considered more appropriate than the parsimonious model.

Diagnostics for lack of fit

Recently, R. Latour (VIMS, P.O. Box 1346, Gloucester Point, VA 23062, U.S.A., personal communication) suggested looking at residuals as a diagnostic tool for assessing tagging models. We analyzed the residuals of the selected model for patterns that would indicate the problems described by Latour.

Results and discussion

The number of legal-sized lobsters tagged in the survey periods ranged from 94 to 577 lobsters; the number of recaptures from the tagged cohorts ranged from 6 to 129 (Table 3).

Table 3. Tag and recapture details of male and female legal-sized lobsters from May 1992 to September 1997.

				Recapture period															
Year and			No.	1992	1993			1994			1995			1996			1997		
timing	Tag date	Sex	tagged	Sept.	Feb.	May	Sept.	Feb.	May	Sept.	Feb.	May	Sept.	Feb.	May	Sept.	Feb.	May	Sept.
1a	May 1992	M	333	13	26	23	5	4	6	1	0	1	2	0	0	0	0	0	0
		F	220		20	12		8	2		1	1		1	0		1	0	
2b	Sept. 1992	M	486		53	27	5	15	13	6	4	2	1	0	1	2	0	0	0
		F	577		36	22		19	14		12	3		1	2		2	0	
2d	Feb. 1993	M	280			15	6	6	10	1	9	2	1	1	0	2	0	0	0
		F	240			10		16	7		11	7		0	0		1	1	
2a	May 1993	M	181				3	21	9	0	4	3	1	3	0	0	0	0	1
		F	105					17	8		5	1		4	1		0	2	
3b	Sept. 1993	M	226					15	6	1	6	3	9	1	1	0	1	0	0
		F	228					21	10		4	5		4	2		0	0	
3d	Feb. 1994	M	357						22	0	17	6	6	2	2	3	0	0	0
		F	323						14		21	6		7	4		1	2	
3a	May 1994	M	229							5	16	13	8	2	5	3	0	1	0
		F	154								11	5		2	2		1	0	
4b	Sept. 1994	M	168								12	16	5	2	3	2	0	0	1
		F	224								8	11		7	2		1	0	
4d	Jan. 1995	M	267									17	6	8	3	10	1	0	0
		F	230									19		7	5		12	1	
4a	May 1995	M	159										8	11	7	11	0	0	2
		F	94											3	3		0	0	

Note: a, after female fishing year; b, before start of male and female fishing year; d, during female and male fishing year. Blank spaces in the recapture part of the table indicate that no fishing occurred for that sex for that period in time.

Table 4. Dispersion coefficients ($\hat{c}$), ΔQAIC values, AIC weights (wQAIC), and level of support for two groups of models based on two (2×) and three (3×) tagging events per year.

Group	Model	$\hat{c}$	ΔQAIC	wQAIC	Support
3×	S–yA	2.05	3.02	0.07	4.53
	S–yC	2.15	0.10	0.29	1.05
	Ct–yA	2.14	4.35	0.03	8.81
	Ct–yC	2.18	4.32	0.03	8.69
	Ce–yA	2.11	0.00	0.30	1.00
	Ce–yC	2.15	0.19	0.27	1.10
2×	S–yA	1.92	4.12	0.06	7.84
	S–yC	2.41	5.57	0.03	16.23
	Ct–yA	1.95	0.00	0.43	1.00
	Ct–yC	2.20	3.08	0.09	4.67
	Ce–yA	1.96	0.52	0.33	1.30
	Ce–yC	2.20	3.90	0.06	7.06

Note: A QAIC is quasi-likelihood adjustment of the AIC value to account for overdispersion of the data. A ΔQAIC value is the difference between the QAIC value for a model and the smallest QAIC value for any model in the group (see Burnham and Anderson 1998 for further details). See Table 2 for model descriptors. Models with support values less than 2 are considered plausible models.

Model selection

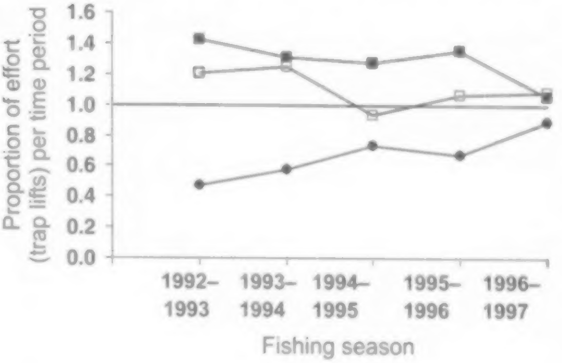
Data for all models were found to be overdispersed and quasi-likelihood adjustments of the AIC values were undertaken (see Burnham and Anderson 1998) (Table 4).

Two groups of models used equivalent amounts of data and model selection within these groups was based on their AIC weights (Burnham and Anderson 1998) (Table 4). The 2× group was based on considering two tagging events per year (September and May) and the 3× group was based on three tagging events per year (September, February and May). In the 3× group, models 3×-Ce–yA, 3×-S–yC, and 3×-Ce–yC had support values less than 2, as had models 2×-Ct–yA and 2×-Ce–yA in the 2× group (Table 4). These models should be considered plausible models for the northwest Tasmanian tag recapture data.

Common to both groups was the Ce–yA model, which estimates annual fishing mortalities with sexes combined based on effort. The other model supported in the 2× group was the model estimating annual fishing mortalities with sexes combined based on the duration of the fishing years. This is not surprising because when the February tagging event is eliminated, the fishing period for males is reduced from 3 (Nov.–Feb., Feb.–May, May–Aug.) to 2 (Nov.–May, May–Aug.) periods and from 2 (Nov.–Feb., Feb.–Apr.) to 1 (Nov.–Apr.) period for females (Table 1). Although a model based on separate sexes was given support in the 3× group, the addition of the extra parameter (sex effect) did not have a substantial improvement over the most parsimonious model and this model is not considered further.

In the 3× model group, fishing mortality estimates with sexes combined based on length of the fishing periods were poorly supported, indicating that the extra tagging period (February) split a period when fishing effort was disproportional to time. There are differences in effort between tagging periods, with the period between the second and third tagging surveys (Feb.–May) having the greatest effort expended per unit of time (Fig. 2). In contrast, the period between the third and first tagging surveys of the following year (May–Sept.) had less effort per unit of time. Over the survey periods, the May to September period has shown a steady increase in the amount of effort expended per unit of time, which reflects the increase in price paid over time for lobster during this period (Frusher 1997). Effort is considered the most appropriate means of partitioning fishing mortalities within a fishing year.

Fig. 2. Comparison of fishing effort expended between September and February (open squares), February to May (solid squares) and May to September (solid circles) for the 1992–1993 to 1996–1997 fishing years. The horizontal line shows were the proportion of effort is equivalent to the proportion of time.



The models producing annual estimates of fishing mortalities with fishing mortality within a year based on fishing effort were considered the most appropriate models for describing the dynamics of the lobster stocks in northwest Tasmania. As the 2×-Ce–yA and 3×-Ce–yA models used different amounts of data, model selection was based on the relative standard errors of the parameters being estimated. In all cases the model based on three tagging events per year had lower relative standard errors than the model based on two tagging events per year.

Model fit

The residuals from the fitted models (e.g., Table 5) display none of the symptoms of problems described by R. Latour (VIMS, P.O. Box 1346 Gloucester Point, VA 23062, U.S.A., personal communication) (i.e., row effects and diagonal effects). There is a preponderance of negative residuals, however, and some columns contain residuals predominantly of the same sign. Latour was unable to generate this kind of column pattern in his simulations though they specifically tried to produce this effect. The model considered here is more complex than the model of Hoenig et al. (1998), which was investigated by Latour (VIMS, P.O. Box 1346 Gloucester Point, VA 23062, U.S.A., unpublished data). Thus, there are potentially more ways that problems could occur. For example, if the residuals for females were of the opposite sign to those of males in a particular recovery year, it might suggest that the molting season for females was unusually early or late relative to molting of males in that year. This does not appear to be the case here. Like Latour, we are unable to suggest a mechanism that would

Table 5. Recapture residuals (observed – expected recaptures) of male and female legal-sized lobsters from May 1992 to September 1997 for the 3×–Ce–yA model.

Year and timing	Tag date	Sex	No. tagged	Recapture period															
				1992	1993			1994			1995			1996			1997		
				Sept.[*]	Feb.[†]	May[‡]	Sept.	Feb.	May	Sept.	Feb.	May	Sept.	Feb.	May	Sept.	Feb.	May	Sept.
1a	May 1992	M	333	1.3	5.5	8.3	0.6	**–3.0**	1.1	**–1.1**	**–2.0**	**–1.7**	1.1	**–0.5**	**–0.6**	**–0.3**	**–0.1**	**–0.1**	**–0.1**
		F	220		3.9	1.1		1.2	**–2.5**		**–1.5**	**–2.0**		**–0.0**	**–1.1**		0.7	**–0.3**	
2b	Sept. 1992	M	486		17.5	1.4	**–2.6**	2.8	4.5	2.4	0.6	**–2.7**	–0.5	**–0.9**	**–0.1**	1.5	**–0.2**	**–0.2**	**–0.2**
		F	577		**–6.2**	**–6.7**		1.1	2.2		5.4	**–4.9**		**–1.7**	**–1.0**		1.2	**–0.7**	
2d	Feb. 1993	M	280			**–7.1**	**–0.6**	**–4.6**	2.6	**–2.1**	6.0	**–2.1**	–0.3	0.2	**–1.0**	1.6	**–0.2**	**–0.2**	**–0.1**
		F	240			**–7.9**		4.8	**–0.4**		6.9	2.1		**–1.7**	–1.9		0.5	0.6	
2a	May 1993	M	181				**–3.6**	10.4	1.6	**–3.1**	1.0	**–1.1**	–0.3	2.2	**–1.0**	**–0.4**	**–0.2**	**–0.2**	0.9
		F	105					9.6	3.1		2.3	**–2.3**		2.9	**–0.2**		–0.3	1.7	
3b	Sept. 1993	M	226					**–1.0**	–5.1	–3.7	1.5	**–3.2**	7.0	**–0.2**	–0.4	–0.6	0.7	**–0.2**	–0.2
		F	228					4.9	**–0.6**		–1.9	–2.1		1.6	**–0.7**		**–0.7**	–0.6	
3d	Feb. 1994	M	357						**–3.92**	–10.9	6.5	**–8.4**	1.4	**–0.8**	–1.4	1.6	**–0.6**	–0.6	–0.5
		F	323						**–8.2**		8.7	**–8.8**		1.9	**–1.6**		**–0.5**	0.7	
3a	May 1994	M	229							**–5.5**	5.9	**–0.8**	3.6	**–0.7**	1.8	1.7	**–0.6**	0.5	**–0.5**
		F	154								2.4	**–5.3**		**–1.5**	–1.9		**–0.0**	–0.9	
4b	Sept. 1994	M	168								2.7	3.2	0.9	**–0.5**	0.0	0.8	**–0.5**	–0.5	0.6
		F	224								**–4.4**	**–4.0**		1.9	**–3.6**		**–0.5**	–1.3	
4d	Jan. 1995	M	267									**–10.3**	–2.7	2.7	**–3.3**	7.4	**–0.1**	**–1.1**	**–0.9**
		F	230									**–1.6**		–0.0	–2.8		10.0	**–0.8**	
4a	May 1995	M	159										**–1.7**	5.1	**–0.1**	8.1	**–1.3**	**–1.2**	1.0
		F	94											**–1.8**	**–2.4**	**–1.4**	**–1.3**		

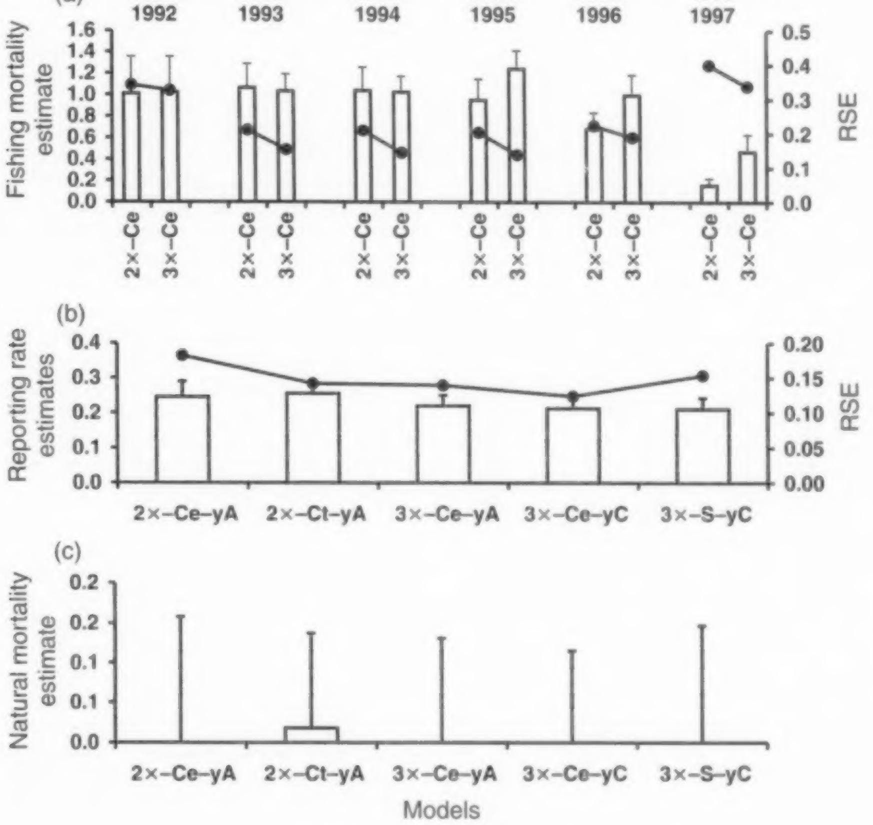
Note: Negative residuals are in bold. a, after female fishing year; b, before start of male and female fishing year; d, during female and male fishing year. Blank spaces in the recapture part of the table indicate that no fishing occurred for that sex for that period in time.

[*] Period from mid-May to mid-Sept. Actual dates are given in Table 2.

[†] Period from mid-Sept. to mid-Feb. Actual dates are given in Table 2.

[‡] Period from mid-Feb. to mid-May. Actual dates are given in Table 2.

Fig. 3. Comparison of (*a*) instantaneous fishing mortality rate, (*b*) tag reporting rate, and (*c*) instantaneous natural mortality rate estimates from 2× and 3× models. Bars give estimated parameters with one standard error. Connected dots show relative standard error (RSE). Meaningful RSE estimates could not be obtained for natural mortality estimates because they approached zero.



generate a column effect. We suggest this may be an important area for research.

A reviewer of the manuscript suggested that certain cells of the recovery matrix with large residuals might be exerting an undue influence on the estimates. We examined the table of residuals (Table 5) for evidence of a problem and tried fitting the model after deleting cells for which the residuals were large (>5). After deleting these cells, there were only minor changes in the parameter estimates. Exploitation rates for the 1991–1992 to 1993–1994 fishing years increased from 64% to 67% and declined for the 1994–1995 (71% to 65%), 1995–1996 (63% to 52%), and 1996–1997 (37% to 18%) fishing years. The larger differences for the last two fishing years are considered to be due to the low number of tags returned after tagging ceased in May 1995, as previously described. Tag reporting rate increased from 22% to 24% and natural mortality remained at zero. The precision of all estimates decreased after the cells with large residuals were removed and there was no change in the column effects of the residuals.

We conclude that although there are some patterns in the residuals, the cause is unclear, as is how the unidentified problem might bias the results. However, as discussed below, the overall results are consistent with those results obtained from the assessment model of Punt and Kennedy (1997), so there is reason to believe that the model has provided reasonable results.

Fishing mortality

Tagging during this study commenced part way through the 1991–1992 fishing year in May 1992. The female component of this fishing year had already closed and thus fishing mortality estimates are based on males for 1991–1992. Only 17% of the fishing effort for the 1991–1992 fishing year was expended between May and September 1992, thus male fishing mortality for this period is based on recaptures from limited effort.

Comparison of the relative standard error (RSE = SE/estimate) of the supported models, which estimated annual fishing mortalities, showed that the 3×-Ce model provided the most precise estimates for all fishing years (Fig. 3*a*).

The fishing mortality estimates for the 1991–1992 to 1993–1994 fishing years were similar. Fishing mortality estimates for 1994–1995 to 1996–1997 were greater for the 3× than 2× models. The 2× model showed a decline in fishing

Fig. 4. Comparison of annual fishing effort and fishing mortality estimates from (*a*) the 3× model and (*b*) the 2× model based on time (open bars) and effort (solid bars). Histogram provides estimated fishing mortality with one standard error. Connected dots show effort.

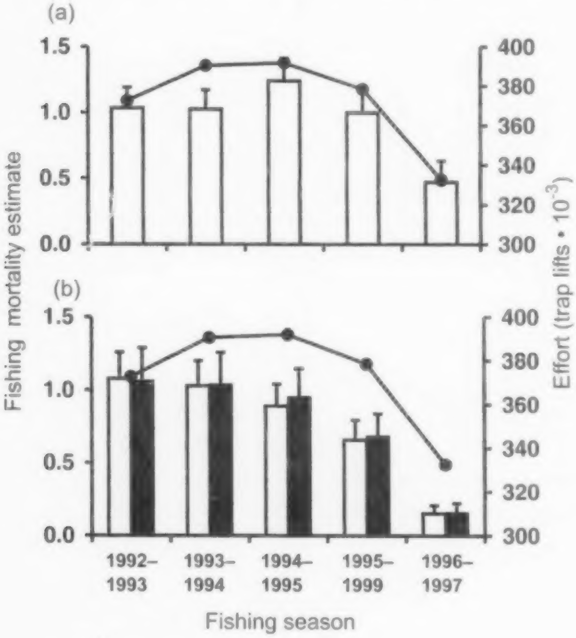


Table 6. Instantaneous fishing mortality rates (F, year^{-1}), exploitation rates ($u = 1 - e^{-F}$), annual catches (C) and estimated biomass ($B = C/u$) from the 3×–Ce–yA model.

Fishing season (Nov.–Aug.)	F	u	C (tonnes)	B (tonnes)
1991–1992	1.02	0.64	431.7	674.5
1992–1993	1.03	0.64	364.8	566.5
1993–1994	1.03	0.64	392.2	611.9
1994–1995	1.24	0.71	362.1	509.2
1995–1996	1.00	0.63	360.4	571.1
1996–1997	0.47	0.38	325.8	866.6

mortality estimates from 1993–1994, whereas this was only apparent in the 1996–1997 fishing year for the 3× model.

Fishing effort is often used as a measure of relative fishing mortality. Fishing effort for the region where tagging was undertaken is available from 1992 onwards. Trends in fishing effort are comparable to the fishing mortality estimates from both models, although the 3× model appears to be a better relative comparison (Fig. 4). Only in the 1996–1997 fishing year was the trend in effort substantially differentfrom the trend in annual fishing mortality estimates, whereas the last two fishing years diverge from the effort trend in the 2× model.

The precision (equivalent to RSE) of the estimates for the most recent years declines with the 1996–1997 estimates being approximately half as precise as the earlier fishing year estimates (with the exception of the 1991–1992 fishing year, when the estimate was based on 17% of the fishing effort). The declining precision for the last fishing years is likely to be due to the low number of tags returned during this period as tagging ceased in May 1995 when exploitation rates remained high. In the fishing year (1995–1996) immediately after tagging ceased, 60% of the tagging event recapture period strata had 2 or fewer returns. In the 1996–1997 fishing year, this increased to 98%, with 66% having zero returns (Table 3).

The most precise estimates were obtained from the 3×–Ce–yA model. These estimates are high with annual harvesting of between 60% and 70% of the legal-sized biomass for all fishing years except the last (Table 6). Although high, these estimates are similar to those found by Frusher et al. (1998) for other regions of Tasmania and have similar trends to biomass estimates obtained from a rock lobster assessment model (Punt and Kennedy 1997), with the exception of the final year. The low fishing mortality estimate for the final year is considered to be due to the low expected rate of tag returns, as discussed earlier.

High exploitation rates in the Tasmanian rock lobster fishery are not unexpected, as Frusher (1997) reports legal-sized biomass to be around 6% of the virgin legal-sized biomass. Additionally, the majority of the legal-sized biomass is composed of recent recruits (Frusher 1997).

Tag reporting rate

In the models tested, tag reporting rate was held constant over all years. Although fishers' behavior with respect to reporting tags can vary between years, there were no major fishery policy changes during the period of surveys that might have altered fishers' behaviour.

Reporting rate and its relative precision showed little variation between models and was estimated reasonably precisely (Fig. 3*b*). S.D. Frusher (personal observation) found no tag loss or tag-induced mortality from over 100 lobsters held in aquaria. Treble (1996) found tag loss to be approximately 3% annually for T-bar tags used in the same species. Although these components of the reporting rate parameter are considered to be low, reporting rate estimates were low (0.20 to 0.23), indicating that fisher cooperation in looking for tags and subsequently reporting tags was poor.

Natural mortality

Natural mortality was also held constant over all years. Natural mortality estimates were very close to zero or very low, ranging from 0–0.018·year^{-1} (Fig. 3*c*). However, the standard errors were relatively large. This indicates that the models tested had trouble estimating this parameter. This may be owing to the relatively short period of time that natural mortality was responsible for total mortality (i.e., when the fishery was closed). In the Tasmanian fishery, the female fishing period is closed for approximately half the year. Hearn et al. (1998) expected that their method would work well in a pulse fishery (i.e., when the fishery is open for such a short time that natural mortality can be considered to be negligible during the fishing period) or when applied to a fishery with a short fishing period (i.e., less than four months).

A concern with the very low estimates of M is that they could be highly correlated with tag reporting rate estimates. However, the covariance matrix obtained from SURVIV (White 1983) indicates that this is not the case. We confirmed this by rerunning the model with M fixed at 0.1, 0.15, and 0.2. These resulted in an increase in tag reporting rate of 11%, 18%, and 25%, respectively, and a decrease in Fs by 10%, 15%, and 20%, respectively, for the first three fishing seasons. These variations were smaller for the later years of the study.

Natural mortality has proved to be very difficult to estimate in lobster stocks. Kennedy (1992) tried to estimate natural mortality of female lobsters from long-term (>15 years) recaptures. Although no definitive estimate could be made from the data, he considered natural mortality for the southern Tasmanian females to be 0.1 or less. Hearn et al. (1998) found that their method produced accurate estimates of M when M was high, although large numbers of animals were required to be tagged (>1000) when fishing mortality was low and reporting rate was 50% or less.

Low tag reporting rates and high fishing mortality rates would make a low natural mortality estimate difficult from tag recapture data. The high fishing mortality will result in few tags being available after one period of fishing and, combined with low tag reporting rate, few tags will be available to estimate M. Frusher and Hoenig (2001) found that improved precision in the estimates of M was best achieved by either improving the tag reporting rate or increasing the duration of the tagging events from three to six fishing seasons.

The large standard errors of the natural mortality estimate also indicate that natural mortality is difficult to determine. However, the natural mortality estimates from all models tested were low, which supports the inferences made by Kennedy (1992).

This is the first time these models have been applied to a real situation and the results are encouraging. Fishing mortality estimates had reasonable estimated precision, and the trends matched results from other methods. Although it is possible to estimate fishing mortality in years after the cessation of tagging, this does not appear to work well when fishing mortality is high owing to the tags being "fished out". It is well known that most methods that produce estimates of fishing and natural mortality tend to produce highly correlated estimates. But, the estimated correlations in this study were modest.

This analysis is also the first time that a detailed model with multiple tagging events within a fishing year has been tested. The 3× model with fishing mortality apportioned by fishing effort and with sexes combined appears to be appropriate for estimating fishing mortality in the northern Tasmanian rock lobster fishery. The precision of natural mortality estimates was low, however, all models indicated that natural mortality was low.

Despite the poor reporting rate, relatively precise estimates of fishing mortality could still be achieved. This is important for the northern Tasmanian fishery, where attempts at estimating fishing mortality rate using other methods have been compromised by the frequent molts and extended molting period of the lobsters.

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Appendix A. Derivation of exploitation rate in terms of natural and fishing mortality components and examples of application to a model using three tagging periods.

Notation

λ	a composite parameter that represents the joint probability of three events: (*i*) the probability that a tag will be found and reported to the fisheries biologist, given that the tagged lobster has been harvested; (*ii*) the probability that a tagged lobsters does not die from the tagging process; and (*iii*) the probability that a tag is not shed immediately. λ is assumed to be constant over time.
F_i	instantaneous fishing mortality rate in year *i*.
F_{mki}	instantaneous male fishing mortality in period *k* of year *i*.
F_{fki}	instantaneous female fishing mortality in period *k* of year *i*.
M	instantaneous natural mortality rate. *M* is assumed to be constant over time and equal for both sexes.
N_{mhi}	number of male lobsters tagged and released at time *h* of year *i*.
N_{fhi}	number of female lobsters tagged and released at time *h* of year *i*.
ε_{ih}	fraction of the annual fishing effort expended in period *h* of year *i*.
Δt_h	length of the *h*th period of the year.
$u_i(F_i,M)$	exploitation rate in year *i*. For convenience, this will be abbreviated to u_i when clarity is not affected.
R_{hijk}	number of recaptures of animals tagged in year *i* at time *h* and recaptured in year *j* during period *k*.
$E[R_{hijk}]$	expected value of R_{hijk}.

Let the year be divided into $K = 3$ periods. The exploitation rate in year *i* can be expressed as

$$u_i(F_i, M) = \sum_{k=1}^{K=3} a_{ik} b_{ik} c_{ik}$$

Here, a_{ik} is the fraction of the population surviving to the beginning of period *k*, with $a_{i1} = 1$ and

$$a_{ik} = \exp\left(-M\sum_{h=1}^{k-1}\Delta t_h - F_i\sum_{h=1}^{k-1}\varepsilon_{ih}\right), \quad k > 1$$

The a_{ik} term prorates the natural mortality according to how much of the year has elapsed since tagging, and prorates the annual fishing mortality according to how much of the fishing effort has occurred up to the start of the *k*th period. The b_{ik} term is the fraction dying in period *k*

$$b_{ik} = 1 - \exp(-M\Delta t_k - F_i\varepsilon_{ik})$$

and c_{ik} is the fraction of the deaths in period *k* owing to fishing

$$c_{ik} = \frac{F_i\varepsilon_{ik}}{F_i\varepsilon_{ik} + M\Delta t_k}$$

The following example is based on female lobsters in northwest Tasmania and partitions a year based on fishing periods and tagging events (Table A1). The tagging events are before (*B*), during (*D*), and after (*A*) the fishing year. Fishing periods divide the year into before (*b*), during (*d*1 and *d*2), and after (*a*1 and *a*2) the fishing year. The portions of effort and time are obtained from Table 1. Because recaptures are dependent on the fishery, recaptures are only obtained in periods *d*1 and *d*2.

The expected recoveries in the first portion of the fishing year (*d*1) in year 1 from tagging before the fishing year (*B*) in year 1 is

$$E[R_{1B1d1}] = \lambda N_{1B}\exp(-0.115M)\,(1 - \exp(-0.494F_1 - 0.271M))\left(\frac{0.494F_1}{0.494F_1 + 0.271M}\right)$$

where N_{1B} is the number of lobsters tagged at time *B*, $\exp(-0.115M)$ is the number of lobsters that have survived period *b* (of length 0.115 years), $(1 - \exp(-0.494F_1 - 0.271M))$ is the number of lobsters dying in period *d*1, and $\left(\frac{0.494F_1}{0.494F_1 + 0.271M}\right)$ is the proportion of lobsters dying in period *d*1 from fishing.

The expected recoveries in the second portion of the fishing year (*d*2) in year 1 from tagging before the fishing year (*B*) in year 1 is

$$E[R_{1B1d2}] = \lambda N_{1B}\exp(-0.386M - 0.496F_1)\,(1-\exp(-0.506F_1 - 0.225M))\left(\frac{0.506F_1}{0.506F_1 + 0.225M}\right)$$

where $\exp(-0.386M - 0.496F_1)$ is the number of lobsters that have survived prior to the start of period *d*2 (i.e., survived period *b* and *d*1), $(1 - \exp(-0.506F_1 - 0.225M))$ *is* the number of lobsters dying in period *d*2, and $\left(\frac{0.506F_1}{0.506F_1 + 0.225M}\right)$ is the proportion of lobsters dying in period *d*2 from fishing.

From the second tagging event (*D*) in year 1 there would only be recaptures in year 1 from period *d*2. The expected recovery is

$$E[R_{1D1d2}] = \lambda N_{1D}(1-\exp(-0.506F_1 - 0.225M))\left(\frac{0.506F_1}{0.506F_1 + 0.225M}\right)$$

Note that there is no term for lobsters surviving prior to exploitation of the fishery as tagging commenced within the fishing year. There are no recoveries in year 1 from tagging after the fishing year (*A*). In year 2 there would be expected recoveries from each of the tagging events in year 1 and, depending on the time of tagging, from some tagging events in year 2.

The expected recoveries in period *d*1 of year 2 from tagging events *B*, *D*, and *A* of year 1 and tagging event *B* of year 2 are $E[R_{1B2d1}]$, $E[R_{1D2d1}]$, $E[R_{1A2d1}]$, and $E[R_{2B2d1}]$, respectively, and are as follows:

$$E[R_{1B2d1}] = \lambda N_{1B}\exp(-1.164M - F_1)\,(1-\exp(-0.509F_2 - 0.238M))\left(\frac{0.509F_2}{0.509F_2 + 0.238M}\right)$$

$$E[R_{1D2d1}] = \lambda N_{1D}\exp(-0.778M - 0.506F_1)\,(1-\exp(-0.509F_2 - 0.238M))\left(\frac{0.509F_2}{0.509F_2 + 0.238M}\right)$$

$$E[R_{1A2d1}] = \lambda N_{1A}\exp(-0.526M)\,(1-\exp(-0.509F_2 - 0.238M))\left(\frac{0.509F_2}{0.509F_2 + 0.238M}\right)$$

$$E[R_{2B2d1}] = \lambda N_{2B}\exp(-0.164M)\,(1-\exp(-0.509F_2 - 0.238M))\left(\frac{0.509F_2}{0.509F_2 + 0.238M}\right)$$

Table A1. Terminology of fishing and tagging periods used in the text and example of apportionment of effort and time for two fishing years.

		B	*b*	*d*1	*D*	*d*2	*a*1	*A*	*a*2
Season	Apportionment	Tag (Sept.)	Fishing closed (Sept.–Nov.)	Fishing open (Nov.–Feb.)	Tag (Feb.)	Fishing open (Feb.–Apr.)	Fishing closed (May)	Tag (May)	Fishing closed (May–Sept.)
1992–1993	Effort		0	0.494		0.506	0		0
	Time		0.115	0.271		0.225	0.027		0.362
1993–1994	Effort		0	0.509		0.491	0		0
	Time		0.164	0.238		0.208	0.027		0.362

Appendix B. Parameter estimability.

In the example in Appendix A, an estimate of *M* can be obtained by dividing $E[R_{1A2d1}]$ by $E[R_{2B2d1}]$, which yields $\frac{N_{1A}\exp(-0.526M)}{N_{2B}\exp(-0.164M)}$ and can be equated with the observed ratio of recaptures R_{1A2d1}/R_{2B2d1}. This is easily solved to obtain an estimate of *M*. Similarly, dividing $E[R_{1B2d1}]$ by $E[R_{1A2d1}]$ or $E[R_{2B2d1}]$ yields $\frac{N_{1B}\exp(-F_1 - 1.164M)}{N_{1A}\exp(-0.526M)} = R_{1B2d1}/R_{1A2d1}$ or $\frac{N_{1B}\exp(-F_1 - 1.164M)}{N_{2B}\exp(-0.164M)} = R_{1B2d1}/R_{2B2d1}$, either of which is easily solved for F_1 once *M* is known. Once *M* and F_1 are known, λ can be obtained from $E[R_{1B1d1}] = R_{1B1d1}$. Similar logic can be used to establish the estimability of all of the parameters in the models considered here.

Properties of abundance indices obtained from acoustic data collected by inshore herring gillnet boats

Ross R. Claytor and Jacques Allard

Abstract: Acoustic data collection during fishing activities can be used to obtain an abundance index. A simulation, calibrated against an experiment conducted during the Pictou, Nova Scotia, Canada, 1997 inshore herring fishery, is used to understand how survey design affects the properties of abundance indices derived from these data. Two fishing survey protocols and random and systematic transect surveys were simulated. During the complete fishing survey protocol, the simulated survey boat collected acoustic data before and after a management-imposed nightly boat limit was caught. In contrast, during the incomplete fishing survey protocol, data collection was terminated when the boat limit was caught. Properties of abundance indices derived from the fishing and transect surveys were examined over five levels of fish dispersion, two conditions of fish mobility, and in the presence and absence of concurrent fleet fishing. All indices were subject to change caused by changing fish dispersion, but only the incomplete fishing survey index was highly unsatisfactory. The complete fishing survey index is more susceptible to change than the transect indices but displays a lower sampling variation across conditions than the transect indices. We conclude that the complete fishing survey index is a viable alternative to the transect indices.

Résumé : La récolte de données acoustiques pendant les activités de pêche commerciale peut servir à établir un indice d'abondance. Une simulation, calibrée d'après une expérience menée durant la saison 1997 de pêche côtière de Harengs à Pictou, Nouvelle-Écosse, Canada, a permis de comprendre comment le plan d'inventaire affecte les propriétés de l'indice d'abondance dérivé de ces données. Deux protocoles d'inventaire de pêche, le transect aléatoire et le transect systématique, ont été simulés. Dans le protocole complet d'inventaire de pêche, le bateau de l'inventaire simulé a récolté des données acoustiques avant et après que le quota de la nuit imposé par les gestionnaires au bateau ait été atteint. En revanche, dans le protocole incomplet, la récolte de données s'est arrêtée lorsque le quota du bateau a été atteint. Les propriétés des indices d'abondance obtenus à partir des inventaires de pêche et les transects ont été examinés sur cinq niveaux de dispersion et deux conditions de mobilité des poissons, ainsi qu'en présence et en absence de pêche par une flottille concurrente. Tous les indices étaient portés à changer d'après la dispersion des poissons, mais seul l'indice obtenu par l'inventaire incomplet était insatisfaisant. L'indice provenant de l'inventaire de pêche complet est plus sujet à changement que les indices obtenus des transects, mais il a une variation d'échantillonnage plus faible dans toute la gamme des conditions d'étude. L'indice obtenu à partir de l'inventaire de pêche complet est donc une alternative acceptable aux indices dérivés des transects.

[Traduit par la Rédaction]

Introduction

Fish population abundance indices and biomass estimates are fundamental to fisheries management. Furthermore, there is increasing evidence of the desirability of tailoring fisheries management to population or metapopulation components of fish stocks in general (Hilborn and Walters 1992; Cooper and Mangel 1999) and for herring stocks in particular (Sinclair 1988). Data obtained from acoustic equipment installed on fishing boats during normal fishery operation have been used to construct abundance indices of herring spawning components (Claytor and Clay 2001). The object of this paper is to study the properties of these indices to determine their utility for fisheries management.

There are several reasons to examine indices and estimates obtained from fishing fleet acoustic data. First, availability and cost limit the usage of government surveying boats. For example, in the southern Gulf of St. Lawrence, several spawning components are fished at the same time in discrete spatial locations over periods ranging from 4 to 6 weeks (Chadwick and Claytor 1989). As a result, it is impossible for the one available government boat to survey each component. Second, fishing boats are located in the area of interest and are readily available for surveys or data collection during fishing activity. Third, fishers have an interest in the management of the resources and are motivated to collect data relevant to their fisheries. Fourth, such an ap-

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proach is beginning to be used, in particular, for the southern Gulf of St. Lawrence herring fishery (Claytor and Clay 2001). Therefore, understanding the properties of abundance indices derived from these data is essential.

We describe several abundance indices of herring that can be derived from gillnetters' acoustic sampling. We examine the impact of fish dispersion, fish mobility, and fish depletion by fleet fishing on the functional relationship between the index and abundance. In particular, we show that this relationship is affected by fish dispersion and mobility. We also examine the sampling variation of the indices.

We develop a computer simulation of fish and fisher behaviour in a gillnet fishery on spawning herring aggregations to study these indices. The reference data used to validate the simulation is provided by an experiment conducted on the 1997 Pictou herring spawning ground fishery in the southern Gulf of St. Lawrence (Claytor and Clay 2001). The small scale of this fishery makes it suitable for this first effort in studying the properties of indices derived from acoustic data collected during regular fishing activity.

We begin by defining an abundance index and describe the relationship with an abundance estimator. We then describe the model, the data used for its validation, and the results. In the Discussion, we make recommendations concerning the most appropriate ways to collect the necessary data from fishing boats and the information costs and consequences of deviating from these recommendations.

Materials and methods

Abundance indices and estimators

An abundance index I is a value that is related to abundance A by the nondecreasing function $I = f(A) + \varepsilon$, where ε is an error term resulting from sampling variation. An abundance estimator $\hat{A}$ can be obtained from an abundance index if the function f is known and can be inverted: $\hat{A} = f^{-1}(I) + \varepsilon'$. For example, the raw results (after calibration) of an acoustic survey of herring give an abundance index I; scaling this index transforms it into an abundance estimator $\hat{A} = f^{-1}(I)$, where f^{-1} is the application of the scaling. Of course, an abundance estimator $\hat{A} = A + \varepsilon$ is also an abundance index.

The best abundance indices are those that are proportional to the abundance $I = kA + \varepsilon$, where k is the proportionality constant and the error is purely random. For such indices, we define robustness to mean that the constant k and the distribution of ε are independent of fish behaviour, fishers' behaviour, and other factors.

Catch rates, defined as catch-per-unit-effort (CPUE), are often the only abundance index available for a fishery (Quinn and Deriso 1999). However, the critical requirement of a proportional relationship,

$$U = q\bar{N} \tag{1}$$

where U is the CPUE (I above), $\bar{N}$ is the average abundance (A above), and q is the catchability coefficient (k above), fails in many circumstances. Analyses assuming a proportional relationship between abundance indicators and stock size will overestimate biomass when the relationship is truly nonproportional and hyperstable (Walters and Pearse 1996). For example, at high abundance, CPUE may be limited by gear or boat capacity and become independent of abundance (Saville and Bailey 1980). Harley et al. (2001), in an examination of 297 CPUE data sets, presented strong evidence that the assumption of proportionality is violated for trawl-type gears. CPUE may also remain high as the area occupied by the stock decreases. Cook and Armstrong (1985) noted that the effects on catchability as a stock contracts can only be assessed by having data on the efficiency of the fleet or the area of stock distribution. Hence, determining stock area can be expected to improve assessments of biomass levels and interpretation of catch rates (Beddington and Rettig 1984). Petitgas (1998) determined that the way in which the fleet samples the density of fish in an area as density changes could have a major effect on interpretations of CPUE. As a result, there is a requirement for robust indices that are based on stock density and area of stock distribution. Acoustic data collected nightly by the herring fishing fleet have the potential to provide such robust indices. We use a computer simulation, calibrated against a field experiment from the 1997 Pictou inshore herring fishery, to evaluate the robustness of these indices.

The 1997 Pictou field experiment

We use the data from an experiment carried out on the spawning grounds of the gillnet fishery in the southern Gulf of St. Lawrence, Pictou, Nova Scotia, Canada (Fig. 1; Clay and Claytor 1998; Claytor and Clay 2001). This area is fished by a fleet of up to 124 boats, which are limited to a length of 13.7 m. Boats are subject to a nightly catch limit of 7000 kg. During the experiment year, the average number of nets used per gillnetter per night in this fishery was 5, and the fishery took place from September 7 to 29, 1997.

The data collection system on board the gillnetter *Broke Again* consisted of a 120-kHz transducer with a 14° beam angle, a transceiver (Femto DE9320 digital echo sounder; Femto Electronics Ltd., Lower Sackville, N.S.), and a computer for logging data. The software used to collect and process the acoustic data was the Hydroacoustic Data Processing System (HDPS; Femto Electronics). Calibration of the acoustic hardware consisted of a ball and time varied gain calibration and proceeded as described by Clay and Claytor (1998). The captain turned the acoustic unit on when the boat left port and turned it off when the boat returned to port. The captain did not have access to the data and conducted his fishing as usual, using his own sounding equipment.

Target strength (TS, kg^{-1}) was estimated using the relationship determined by Foote (1987):

$$\mathrm{TS}_{\log} = (20\log_{10} l - 71.9) - 10\log_{10} w \tag{2}$$

where l is length (cm) and w is weight (kg). Samples for estimating length and weight of the acoustically recorded herring were obtained from experimental gillnets consisting of six mesh sizes from 51 mm to 76 mm.

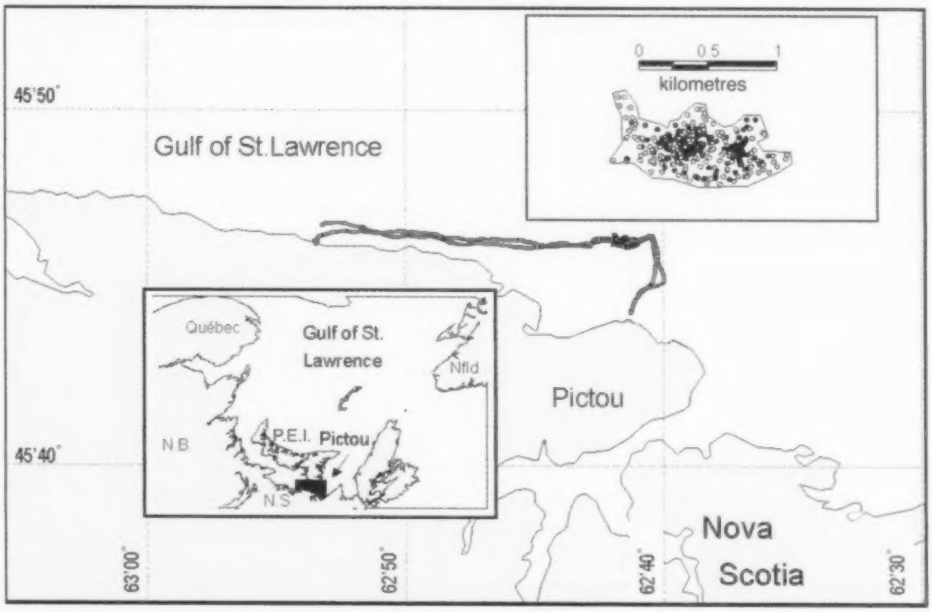
The fishing track was identified by recording latitude and longitude once per second using a Garmin 45XL portable GPS unit (Garmin International Inc., Olathe, Kansas). The fishing track was divided into 100-m increments. A datum point was the average density and geographic position along the increment (Fig. 1). CPUE was calculated as the catch divided by nets ($kg \cdot net^{-1}$) for the survey boat and all fleet boats. Details of the field experiment are in Claytor and Clay (2001) and Claytor (2001).

We required a simulation model that was compatible with knowledge of the behaviour of the fish and the fishers obtained from the field experiment. This requirement imposed choices in the simulation design parameters, as described above, whereas other parameters were estimated in the simulation and were, therefore, consequences of the design choices.

Simulation

The model simulates (*i*) the search area, (*ii*) the herring stock, (*iii*) the foraging behaviour of the fisher, (*iv*) the fishing fleet, and (*v*) the four sampling methods. These elements are better described individually. In the following description, unless otherwise indicated, a "random" value means a value selected using a uniform random variable over the range specified. A survey is defined as

Fig. 1. Location of Pictou, Nova Scotia, Canada, herring gillnet fishery 1997 field experiment. Location of the experimental area within the southern Gulf of St. Lawrence is indicated in the lower inset. A detail of the herring school where searching and fishing occurred is shown in the upper inset. Solid circles, locations where density $\geq 0.0625\ \text{kg}\cdot\text{m}^{-2}$; open circles, locations where density $< 0.0625\ \text{kg}\cdot\text{m}^{-2}$. Canadian provincial abbreviations: N.B., New Brunswick; N.S., Nova Scotia; P.E.I., Prince Edward Island; Nfld., Newfoundland.



any method for collecting acoustic data. A survey boat is a boat like the gillnetter *Broke Again* or the simulated fishing boat that collects acoustic data during regular fishing activity. Complete details of the simulation model are provided in Claytor (2001).

Search area

The simulated search area was scaled to a 700 m × 700 m square. A Euclidean coordinate system in metres with the origin at the southwest corner of the square was used. The total time for data collection was set to 4 h divided into time units of 0.015 h. Fishing and searching decisions were made in multiples of these time units. These parameters were design decisions based on the experimental field data (Table 1).

The herring stock

The herring stock was composed of 1 to 10 clusters. Each cluster was centred on a point inside the search area but 100 m away from its boundary to ensure that only relatively low densities were outside the search area. The location of the cluster centres was randomly selected. The biomass density of the school was defined by a binormal density function of (x,y) with a covariance matrix equal to a multiple $c^2\mathbf{I}$, where $\mathbf{I}$ is the 2 × 2 identity matrix. As a result, cluster density had a radial symmetry around the cluster centre. The biomass density was scaled so that total biomass was approximately equal to preset values ranging from 50 to 15 000 t (tonnes) for the search area.

Varying c allows the school to be more or less dispersed. A dispersion scale, simply referred to as the dispersion, was defined as the smallest area containing 75% of the biomass, divided by 0.75 times the search area. For example, if 37.5% was the smallest area containing 75% of the biomass, then the dispersion would be 0.5. Therefore, the dispersion varies between 0, all fish are at the same location, and 1, the fish are uniformly dispersed (compare with Swain and Sinclair (1994) and Swain and Morin (1996)). We varied c and the number of clusters so that the smallest areas containing 75% of the biomass were 2, 37.5, 50, 67.5, and 75% of the search area, corresponding to dispersions of 0.03, 0.50, 0.67, 0.90, and 1.00, respectively (Fig. 2).

Surveying mobile and immobile populations compared the effects of simulated fish mobility. Fish mobility was simulated by moving the cluster centres at 5-min intervals in a random direction and at a random distance between 0 and 200 m. The speed and time intervals were chosen to represent realistic movement of herring in the area, but they do represent a compromise between computing time and realism. Herring schools have been found to migrate an average of about two-thirds of a body length per second (Hafsteinsson and Misund 1995). The average body length of southern Gulf of St. Lawrence herring is about 0.30 m (Claytor et al. 1998). Moving 200 m every 5 min would correspond to about $0.67\ \text{m}\cdot\text{s}^{-1}$ or about two body lengths per second. This speed should present a good test of the method with respect to fish movement. If a particular random displacement placed the cluster centre within 100 m of the boundary, a different random displacement was tried.

Foraging behaviour of the fisher

The turning decision rules and simulated fishing patterns were derived from direct on-board experience of the first author. The survey boat entered the area at a random point on the x or y axes. Its acoustic equipment was recording at all times except during simulated fishing. The boat path was divided into 100-m increments. The density was numerically integrated over each increment.

The simulated fisher used either a random searching mode or a directed searching mode. During random searches, the boat could turn every 200 m. The turning angle was obtained using a uniform random variable between 0 and 360 degrees. The boat was in random search mode for the initial 20 time periods after entering the fishing area. During directed searches, the boat could turn every 100 m. The turning decision was based on a set of rules depending on the acoustic data available. The direction of the turn was based

Table 1. Design and estimated parameters used to set and validate simulation.

Parameter	Type	Field experiment			Simulation		
		Minimum	Average	Maximum	Minimum	Average	Maximum
Search time (h)	Design	1.6	4.3	10.8	0.3	2.5	4.0
Search area $(\text{m}^2\cdot 10^3)$	Design	64	404	710	195	316	400
Search distance $(\text{m}\cdot 10^3)$	Design	5.3	22.1	40.7	0.8	4.8	24.2
Stock size (t)	Design	50	1170	3931	50	3143	15 000
Number of boats	Design	24	68	124	10	87	120
Survey boat catch (kg)	Estimated	827	5629	7058	374	6082	7 500
Fleet catch $(\text{kg}\cdot 10^3)$	Estimated	63	373	767	5	424	759
Sets at low density (no.)	Estimated	1	3.2	5	2	5.2	7
Sets at high density (no.)	Estimated	1	2	3	1	1.7	4
CPUE survey boat $(\text{kg}\cdot\text{net}^{-1})$	Estimated	165	1126	1412	74	1216	1 500
CPUE fleet $(\text{kg}\cdot\text{net}^{-1})$	Estimated	456	954	1466	74	987	1 490

the slope of the density as a function of distance traveled for the last 100-m displacement. For example, if the slope was positive, higher fish densities were deemed to be ahead and the boat tended to keep going in the current direction. If the slope was negative, lower fish densities were deemed to be ahead and the boat tended to turn back. When the slope was near zero, the boat made a right or left turn at approximately a right angle. The angle of the turn was determined by the magnitude of the slope, whereas the direction (left or right) of the turn was randomly determined. At the end of the 100 m, a decision on turning angle and direction of the turn was made according the following rules.

Slope of the density $(\text{fish}\cdot\text{m}^{-2}\cdot(20\ \text{m})^{-1})$	Turning-angle range (degrees)
<-1	150–180
≥ -1 and <-0.5	120–150
≥ -0.5 and <0	90–120
≥ 0 and <0.5	60–90
≥ 0.5 and <1	30–60
≥ 1	0–30

If at any time a turn took the boat out of the search area, a new angle and direction were randomly chosen until the turn kept the boat in the search area.

Fishing only occurred during a directed search and when certain conditions associated with the density of the stock and the slope were met. Each fishing event took 30 min. During this time, data collection by the boat stopped to simulate the time required for the net to be set and hauled. After each fishing event, the boat would search randomly for 20 time units before beginning the directed search again. Fishing by the survey boat continued until the boat limit was caught or the allotted 4-h time limit was reached. After the boat limit was caught, the survey boat continued to collect data under the searching rules but would not fish.

Fishing by the simulated survey boat removed fish from the overall stock on a cluster-by-cluster basis. Each cluster was depleted in proportion to its contribution to the density at the fishing location. For example, if most of the catch occurred near the centre of one distribution and the edge of another, then the cluster that had the catch near its centre would have more biomass removed from it than the one where catches occurred near the edge.

Fishing fleet

The main purpose for simulating the fishing fleet was to take into account concurrent stock depletion on the proposed indices during the acoustic simulated data collection. As a result, it was not necessary for each individual boat in the simulated fleet to search and fish according to the rules defined for the simulated acoustic boat. This strategy allowed fleet fishing to be modeled using a less computationally intensive approximation of the simulated acoustic boats searching behaviour. Three factors were considered with respect to fleet fishing: (*i*) number of boats fishing on a night, (*ii*) fishing locations of each boat, and (*iii*) the proportion of the boats fishing during each fishing event.

Fleet size randomly varied in proportion to stock size based on empirical data. The constraints on this model were that the minimum number of boats fishing in a night was 10, and the maximum was 120, including the survey boat (Table 1).

We assumed that fishing locations for individual boats in the fleet would be consistent with fishers being able to locate higher than average densities for fishing. This objective was achieved by randomly selecting points with a probability proportional to a power of the fish density, the power being chosen randomly between 0.5 and 1.5. The power randomly changed the ability of the fleet to locate high densities as might be expected during a fishery because of weather or other factors beyond the fishers' control.

Fishing opportunities for the simulated fleet occurred every 30 min during each 4-h trip. Thus, each boat in the fleet had the possibility of making 8 sets a night. However, we designed the simulation so that the average number of sets made by each boat in the fishing fleet and the acoustic survey boat would be equal. To determine how often fleet fishing would occur, we first collected three nights of fishing data from the acoustic survey boat before each simulation and recorded the number of times that the acoustic boat fished. This number was updated throughout the simulation as more data from the acoustic boat became available. During the simulation, we randomly selected fleet boats in such a way that they fished on average as often as the survey boat.

The catch of each boat in the simulated fleet was recorded in a consistent sequence for each fishing event. The catch from each boat in the fishing fleet depleted each cluster as described above for the survey boat. This sequential fishing gradually depleted the stock.

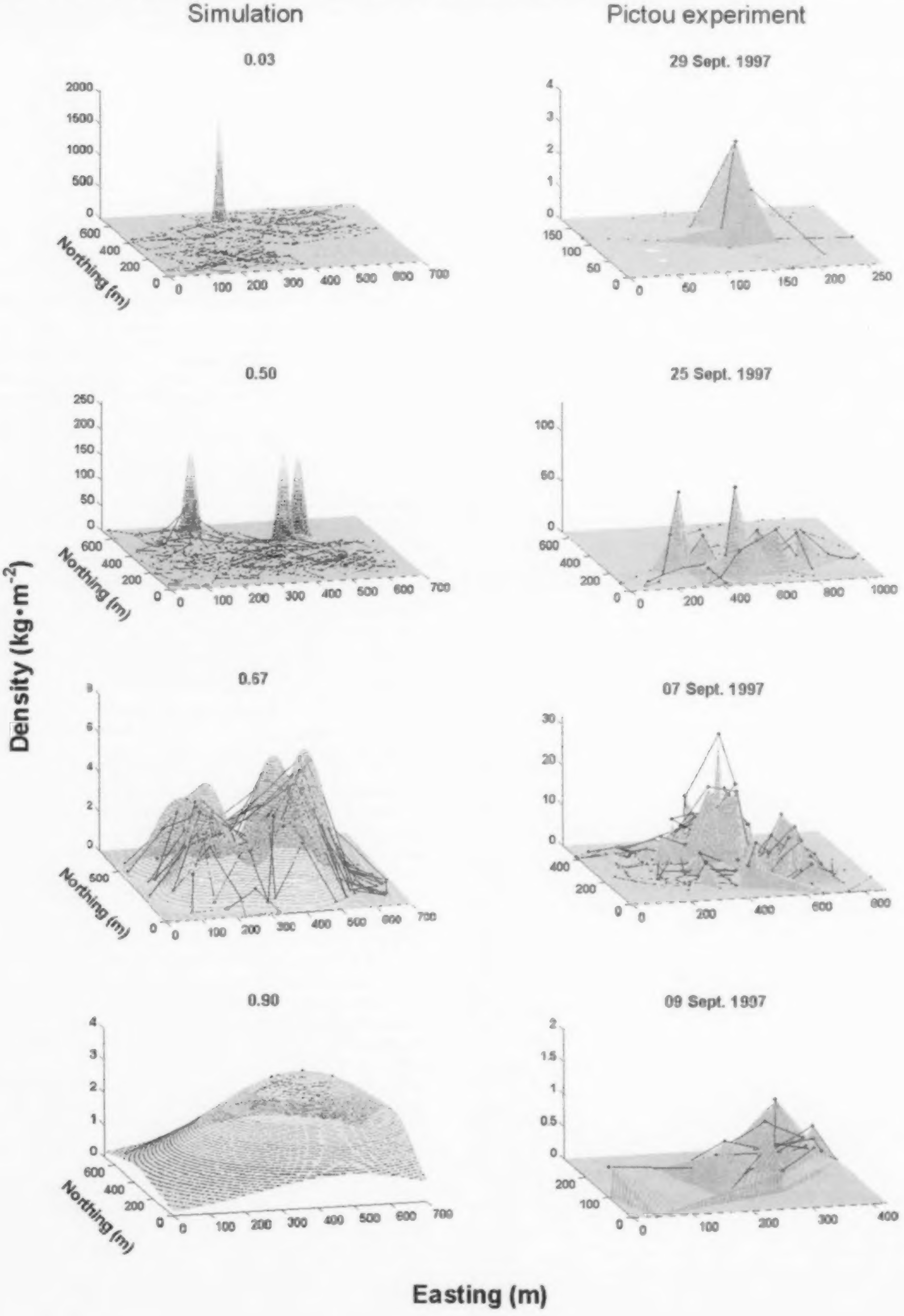
If surveying in the simulation occurs while the fleet is fishing, we describe this as surveying in the presence of concurrent fleet fishing. In contrast, if no fleet fishing occurs during surveying, it is described as surveying in the absence of concurrent fleet fishing.

Sampling methods and computation of biomass indices

The following sampling methods were simulated simultaneously within each 4-hour simulation.

Data were collected along eight equally spaced transects and along eight random transects parallel to the *x* axis and ordered by distance from the origin. In each case, the abundance index was the total biomass that is estimated by multiplying the average of the density for the eight transects by the total simulated search area.

Fig. 2. A comparison of simulated distributions to those observed in the Pictou 1997 experimental fishery. Numbers above simulated distributions indicate the dispersion scale for that distribution (see Materials and methods for details).



Data collection by the simulated survey boats was continuous and each transect required 30 min of simulation time to complete.

The simulated survey boat collected acoustic data while it searched for schools of fishable size. No acoustic data were collected by the fishing boats during the 30 min taken to set and haul the nets. Two cases were simulated: incomplete fishing surveys, where data collection stopped when the boat limit was reached, and complete fishing surveys, where data collection continued for the 4-h period regardless of the catch.

The abundance index from the fishing surveys is the sum of density for each 100-m section weighted by the area of the appropriate Voronoi polygon (see below). CPUE was estimated for the survey boat and the fishing fleet as catch per total number of nets used by all boats under consideration for the index.

Biomass indices from the fishing surveys were computed in the following way. Consider the set of points where data were obtained by the survey boat as the data points. Take the convex hull of the data points (the smallest convex polygon including all of these points) and their barycenter (each coordinate of the barycenter is the average of the corresponding coordinates of the data points). For each vertex on the convex hull, trace a half line from the barycenter through the vertex and take the point 20 m farther from the barycenter. These new points form an expanded convex polygon slightly larger than the convex hull of the data point (Cressie 1991). This expanded convex polygon was considered to be the area occupied by the fish schools as observed during the sampling process. Voronoi polygons around each data point were computed using the MATLAB (1998, ver. 5.3) Voronoi function and intersected with the expanded convex hull. The biomass index was the sum of the densities at each data point weighted by the area of the Voronoi polygon around the data point (Green and Sibson 1978; Boots and Murdoch 1983).

Evaluating performance of indices

The indices described above were derived from each simulation trial. A simulation trial consisted of a 4-h fishing trip. A trial was conducted at each of the 16 stock abundance levels, five levels of fish dispersion, two conditions of fish mobility, and in the presence and absence of concurrent fleet fishing. Each trial was repeated 20 times and data from each of the two fishing survey protocols and random and systematic transect surveys were collected simultaneously during each trial repetition.

After observing that the simulated indices were linearly related to the abundance ($I = k_{\text{conditions}} A + \varepsilon$) for each set of conditions, the dependency of the proportionality constant $k_{\text{conditions}}$ on the conditions was studied.

Similarly, after observing that the standard error, $\sigma(\varepsilon)$, was proportional to abundance for each set of conditions, the relative standard error $\sigma_{\text{conditions}}(\varepsilon)\cdot A^{-1}$ (computed using a 0-intercept regression) was used as the measure of the sampling variation of the index. The relative standard error is a dimensionless number expressing random variation of the index like the coefficient of variation expresses variation in a statistical population.

To evaluate the robustness of these indices, we describe spurious changes in index values caused by changing fish and fishers' behaviour when the abundance is actually constant. For example, a proportionality constant that changed from 1.0 to 0.8 depending on conditions would lead to a spurious relative index indicating a −20% change in population size, but a +25% increase when changing from 0.8 to 1.0. We will describe this as a spurious index change of −20%/+25% when abundance is actually constant. We first evaluate the effect on index values when all conditions are changing, that is, when index values for all possible levels of a condition are combined. Subsequently, we evaluate the effect of each condition changing while the others are fixed on index values.

Results

Validation of the simulation

The design and estimated parameters from the simulation and the 1997 Pictou field experiment were similar (Table 1). For example, the experimental and simulated catch and catch rate patterns were similar for the survey boat and the fleet (Fig. 3). The effect of boat limits on total catches and catch rates was also similar (Fig. 3). The number of sets required for catching the boat limit declined as density increased (Table 1).

Indices

For each set of conditions, we observed that all indices were linear functions $I = k_{\text{conditions}}A + \varepsilon_{\text{conditions}}$ with intercepts through the origin (Fig. 4). Therefore, if a single set of conditions always held, all indices would be proportional to abundance. However, the simulation shows that the proportionality constant $k_{\text{conditions}}$ depends on survey type, fleet fishing, and fish mobility (Table 2). This dependence leads to undesirable characteristics in some of the indices examined.

Index robustness

Effect of simultaneous change in all conditions

The least robust case was the incomplete fishing survey. Changes in fish dispersion, fish mobility, and fleet fishing would mislead a user of this index to conclude that up to a 78% ((1.24 − 0.27)/1.24) reduction or, conversely, a 359% ((1.24 − 0.27)/0.27) increase in abundance had occurred when the abundance was actually constant. We consider that this spurious index change of −78%/+359% makes this survey type unsuitable as a fisheries management tool and will not be discussed further.

When the abundance was actually constant, the other three survey types produced spurious index changes varying between −35 and +136%. Random transect surveys provided the most robust indices to changes in all conditions (Table 3).

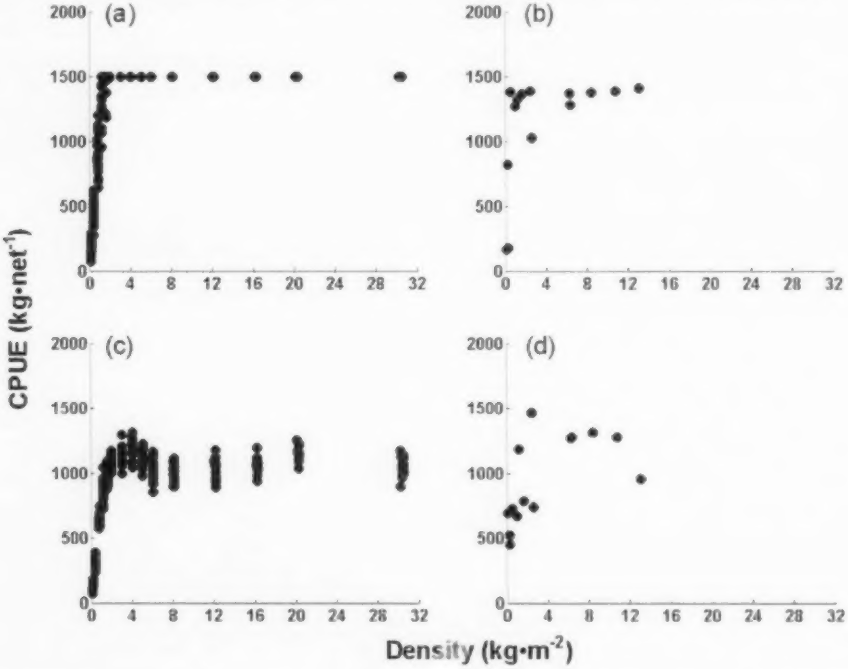
Effect of changes in fish dispersion with fixed concurrent fleet fishing and fish mobility

In general, random transect surveys produced the most robust indices and complete fishing surveys produced the least robust indices to changes in fish dispersion. Spurious index changes up to −47%/+87% occurred for complete fishing surveys (Table 3). However, random and systematic transect surveys were sometimes less robust than complete fishing surveys. For example, surveys of immobile fish in the absence of concurrent fleet fishing using random transects had spurious index changes that were greater then those of complete fishing surveys (Table 3).

Effect of change in fish mobility with fixed fish dispersion and concurrent fleet fishing

Random transect surveys produced the most robust indices to changes in fish mobility (Table 4), and all indices were more robust to changes in fish mobility compared with changes in fish dispersion (compare Tables 3 and 4). All indices were most robust to changes in mobility when the fish were the most dispersed (≥0.67) with spurious index changes <±15% (Table 4).

Fig. 3. A comparison of the catch-per-unit-effort (CPUE) from the simulated survey and fleet boats to the CPUE observed for the Pictou experimental survey boat and the Pictou fleet in the 1997 herring gillnet fishery. Figures are simulated and Pictou experimental results are as follows: (*a*) simulated acoustic boat, (*b*) Pictou experiment – acoustic boat, (*c*) simulated fleet, and (*d*) Pictou experiment – fleet.



Effect of change in concurrent fleet fishing with fixed fish dispersion and fish mobility

Complete fishing survey indices were the most robust to changes in concurrent fleet fishing when dispersion was ≥0.50 (Table 4). However, random transects were the most robust when fish dispersion was least (Table 4).

All indices were more robust to changes in concurrent fleet fishing compared with changes in fish mobility. All indices were least robust to changes in fish dispersion (compare Tables 3 and 4). All indices were least robust when dispersion was least (Table 4). However, we found that robustness of complete fishing and systematic transect surveys were the most predictable with respect to decreasing fish dispersion. That is, as dispersion decreased, robustness also decreased, but random transect surveys were less robust at 0.50 dispersions compared with 0.03 dispersions (Table 4).

Sampling variation of the abundance indices

The standard error, $\sigma_{\text{conditions}}(\varepsilon)$, is proportional to abundance (Fig. 4). Therefore, the relative standard error (sampling variation), $\sigma_{\text{conditions}}(\varepsilon)\cdot A^{-1}$, is constant for a given set of conditions but varies among conditions (Table 5). The sampling variation was highest for the least dispersed fish and for mobile fish.

When fish are least dispersed, sampling variation of the complete fishing survey index was much lower than the random and systematic transect survey indices. For moderately dispersed fish (0.67–0.90), the complete fishing survey index provided excellent results, with a sampling variation independent of fish mobility and lower than that of the random transect indices in all cases and lower than that of the systematic transect indices for mobile fish. For highly dispersed fish, the complete fishing survey index shows a sampling variability slightly higher than that of the transect indices (Table 5).

Discussion

Overall recommendations

A fishery manager or scientist has two main reasons for conducting surveys. First, they may wish to obtain abundance indices to describe population changes. Second, they may want to obtain estimates of absolute abundance. Abundance indices allow decision rules that explicitly or implicitly state the management actions to be implemented when an abundance change of a given magnitude has occurred. For example, if the index indicates a decline, then additional restrictions on effort, seasons, gear, or other mechanisms for limiting catch, which may include quota or allocation reductions, are applied. On the other hand, if the index is increasing, restrictions are lifted. Absolute abundance estimates are used to set minimum biomass targets or fishing levels based on a fixed percentage of the estimated population size.

Abundance estimates derived from abundance indices will have robustness properties and sampling variation similar to those of the index. Therefore, any abundance estimate derived from one of these survey methods will have the same qualitative properties, and our conclusions apply to both indices and estimates.

Clearly, incomplete fishing surveys should not be relied upon to obtain abundance indices. The lack of robustness of

Fig. 4. Scatter diagram of the abundance index compared with the true biomass for distributions with a dispersion of 0.67 for each of the survey methods. The solid line is the regression line and the broken line is the line with unit slope (slope equal to one) shown as visual reference. Figures are for simulated results as follows: (*a*) complete fishing, (*b*) random transect, (*c*) incomplete fishing, and (*d*) systematic transect.

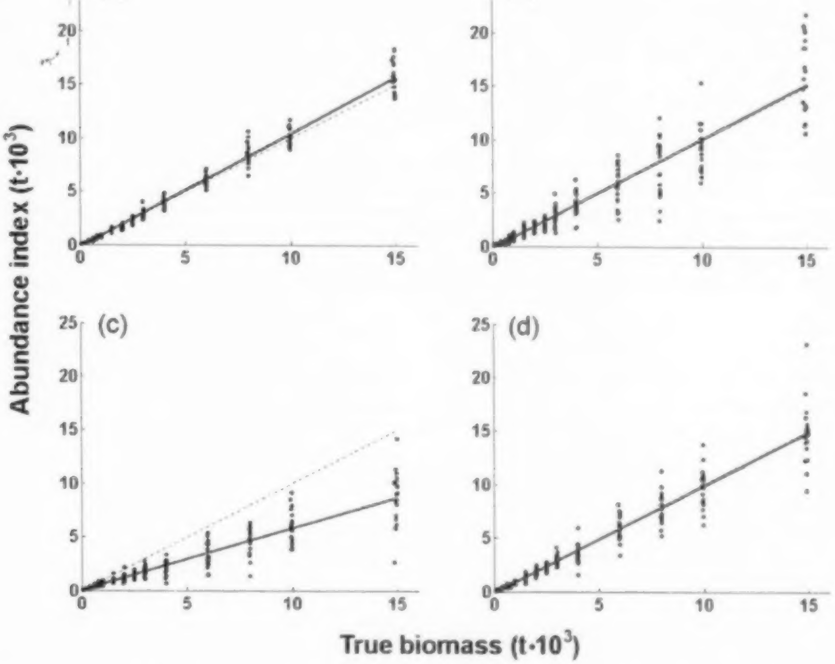


Table 2. Proportionality constant of four abundance indices for each dispersion, concurrent fleet fishing, and mobility condition examined for the four survey types.

		Survey							
	Concurrent	Complete fishing		Incomplete fishing		Random transect		Systematic transect	
Dispersion	fleet fishing	Mobile	Immobile	Mobile	Immobile	Mobile	Immobile	Mobile	Immobile
0.03	Present	1.25	0.71	1.24	1.10	0.91	0.91	0.58	1.03
	Absent	1.44	1.03			0.81	0.83	1.01	1.37
0.50	Present	1.14	0.94	0.74	0.62	0.99	1.05	0.97	0.91
	Absent	1.17	0.98			0.86	1.24	1.14	1.00
0.67	Present	1.06	0.97	0.58	0.46	1.02	1.01	1.00	0.99
	Absent	1.09	0.97			1.00	0.99	1.00	1.00
0.90	Present	0.86	0.78	0.41	0.37	1.05	1.00	1.04	0.99
	Absent	0.86	0.79			0.98	0.99	1.04	1.00
1.00	Present	0.78	0.74	0.27	0.28	1.00	1.00	1.00	1.00
	Absent	0.77	0.74			1.00	1.00	1.00	1.00

Note: Dispersion describes a scale from least dispersed (0.03) to most dispersed (1.0) (see Materials and methods for details).

incomplete fishing survey indices is due to the incomplete spatial and temporal coverage of the population. As a result, development of indices based on data collected during regular fishing activity requires that the entire spatial and temporal area of the stock be surveyed. Spurious results will also be obtained using random and systematic surveys if this criterion is not applied (Hilborn and Walters 1992).

Because changes in fish dispersion have the greatest effect on the robustness of all indices, it is the most important factor to consider when deciding on which survey to use for deriving indices. If dispersion is likely to be changing while the survey is being conducted, random transect surveys would be expected to provide the most robust index. However, because complete fishing surveys and systematic surveys were the most predictable with respect to decreasing fish dispersion, they may be preferable to random transect indices unless extremely low fish dispersions are expected to predominant. In general, the choice of survey type will be

Table 3. Spurious index change resulting from all conditions changing (fish dispersion, fish mobility, and concurrent fleet fishing) compared with fish dispersion conditions changing while concurrent fleet fishing and fish mobility are fixed (in all cases, abundance is constant).

Condition			Survey		
Dispersion	Concurrent fleet fishing	Mobility	Complete fishing (%)	Random transect (%)	Systematic transect (%)
Changing	Changing	Changing	–51/+103	–35/+53	–58/+136
Changing	Present	Mobile	–38/+60	–13/+15	–44/+79
Changing	Absent	Mobile	–47/+87	–13/+15	–12/+14
Changing	Present	Immobile	–27/+37	–13/+15	–12/+13
Changing	Absent	Immobile	–28/+39	–33/+49	–27/+37

Table 4. Spurious index change caused by change in mobility with fixed dispersion and concurrent fleet fishing compared with change in concurrent fleet fishing with fixed dispersion and mobility (in all cases, abundance is constant).

Condition			Survey		
Dispersion	Concurrent fleet fishing	Mobility	Complete fishing (%)	Random transect (%)	Systematic transect (%)
0.03	Present	Changing	–43/+76	–0/+0	–44/+78
0.03	Absent	Changing	–28/+40	–2/+2	–26/+36
0.03	Changing	Mobile	–13/+15	–11/+12	–43/+74
0.03	Changing	Immobile	–31/+45	–9/+10	–25/+33
0.50	Present	Changing	–18/+21	–6/+6	–6/+7
0.50	Absent	Changing	–16/+19	–31/+44	–12/+14
0.50	Changing	Mobile	–3/+3	–13/+15	–15/+18
0.50	Changing	Immobile	–4/+4	–15/+18	–9/+10
0.67	Present	Changing	–8/+9	–1/+1	–1/+1
0.67	Absent	Changing	–11/+12	–1/+1	–0/+0
0.67	Changing	Mobile	–3/+3	–2/+2	–0/+0
0.67	Changing	Immobile	–0/+0	–2/+2	–1/+1
0.90	Present	Changing	–9/+10	–5/+5	–5/+5
0.90	Absent	Changing	–8/+9	–1/+1	–4/+4
0.90	Changing	Mobile	–0/+0	–7/+7	–0/+0
0.90	Changing	Immobile	–1/+1	–1/+1	–1/+1
1.00	Present	Changing	–5/+5	–0/+0	–0/+0
1.00	Absent	Changing	–4/+4	–0/+0	–0/+0
1.00	Changing	Mobile	–1/+1	–0/+0	–0/+0
1.00	Changing	Immobile	–0/+0	–0/+0	–0/+0

based on a balance between application cost and the decline in robustness expected from choosing a particular survey type.

Changes in fish mobility affect all indices to a lesser extent than changes in fish dispersion. Changes in concurrent fleet fishing have the least impact on index robustness. Unless fish have very low dispersion characteristics, the differences in robustness between controlling survey times for mobile versus immobile fish or for the presence or absence of concurrent fleet fishing makes little difference. As a result, surveys in the presence or absence of concurrent fleet fishing and on mobile and immobile fish can be mixed.

McAllister (1998) examined the effect of movement in one direction over relatively large scales and found it to be an important feature to consider when designing a survey. Random movement over the relatively small geographic scale found on the Pictou, Nova Scotia, herring spawning aggregations was not an important factor. His results do indicate, however, that movement over the geographic scales associated with the Gulf of St. Lawrence purse seine fishery will be an important feature to examine (Claytor et al. 2001). Therefore, extrapolation of our results to larger geographic scales is not advisable without additional research.

The complete fishing survey shows the lowest sampling variation across fish conditions. This lower sampling variation is a likely consequence of the searching aspect of the complete fishing survey method and is an important factor in favour of this index. Positive sampling error will lead to overfishing, whereas negative sampling error will lead to economic loss. Thus, wide sampling variations lead to poor fisheries management. Quantifying these errors with respect to long-term yield is an important aspect for future research.

The complete fishing survey has the disadvantage of lower robustness but the advantage of lower sampling variation. These factors must both be considered to determine its advantages for fisheries management. Identifying the cost or consequences of using one survey type over another is important because implementation of random or systematic transect surveys during fleet fishing is often difficult. It is impossible for a fishing boat to search for fish schools of commercial size, set nets, search for the next fishing school, set again, and repeat this sequence until fishing is completed and then survey in such a manner that the entire spatial and temporal extent of the school is covered. If random or systematic transect surveys are to be conducted, the survey boat must only conduct surveys and not engage in fishing activ-

Table 5. Sampling variation ($\sigma_{\text{conditions}}(\varepsilon)\cdot A^{-1}$) of the abundance indices for each dispersion, fishing, and mobility condition examined for the four survey types.

		Survey							
	Concurrent fleet fishing	Complete fishing		Incomplete fishing		Random transect		Systematic transect	
Dispersion		Mobile	Immobile	Mobile	Immobile	Mobile	Immobile	Mobile	Immobile
0.03	Present	1.10	0.51	1.40	1.37	1.64	1.77	1.49	1.32
	Absent	0.90	0.58			1.70	2.00	1.81	1.75
0.50	Present	0.36	0.16	0.63	0.65	0.82	0.73	0.64	0.40
	Absent	0.31	0.16			0.75	0.82	0.77	0.42
0.67	Present	0.09	0.04	0.16	0.18	0.25	0.23	0.19	0.01
	Absent	0.09	0.06			0.27	0.23	0.20	0.00
0.90	Present	0.07	0.07	0.11	0.09	0.11	0.13	0.08	0.05
	Absent	0.07	0.06			0.15	0.10	0.10	0.05
1.00	Present	0.05	0.07	0.08	0.08	0.01	0.01	0.01	0.01
	Absent	0.05	0.06			0.01	0.01	0.01	0.01

ity. This loss of fishing income requires compensation for surveying and not fishing. Thus, being able to directly evaluate the costs and consequences of adopting a particular survey method is important for fishing groups, fisheries managers, and scientists. There may be situations in which these groups will decide that the gain in index robustness is worth the extra cost required to conduct random or systematic surveys rather than complete fishing surveys.

Acoustic measurement sources of error

In this paper, we have exclusively concentrated on survey design aspects of obtaining abundance and exploitation rate indices from acoustic measurements collected by inshore herring gillnet boats. We have assumed that factors related to the estimation of abundance indices using acoustic surveys, such as target strength, variability of backscatter in high target concentrations, vessel avoidance, and acoustic extinction from near-surface reverberation, would be constant regardless of whether data were collected by fishing boats during regular fishing activity or by fishing boats during random or systematic transect surveys. These factors preclude an interpretation of the indices derived from acoustic data as absolute biomass estimates, and we have restricted the interpretation of our results to relative indices of abundance and exploitation rate. Previous work on the acoustic systems that we have placed on board gillnet boats has demonstrated that calibrations are equivalent to those obtained on research vessels currently conducting acoustic surveys of fish populations in Atlantic Canada (Clay and Claytor 1998). Nevertheless, we recognize that the provision of stock assessment advice that is based on acoustic-derived indices requires techniques that incorporate or at least acknowledge that uncertainty arises from survey design and acoustic measurements (Rose et al. 2000) as well as ground truthing and species identification concerns (McClatchie et al. 2000). This recognition of all sources of uncertainty applies regardless of the data collection techniques. For example, a variety of factors also affect abundance indices derived from trawl surveys (Somerton et al. 1999).

Contribution to a new paradigm for managing herring spawning components

The ability to accurately monitor changes in fish stock biomass and exploitation rate allows new paradigms in fisheries management to be tested (Thomas et al. 1997). Developing robust abundance indices from nightly fishery-collected data is important because it creates the possibility for managers to directly measure and test the effects of decisions regarding when and where to fish. These indices provide a mechanism for directly making and implementing decision rules regarding the elimination of high exploitation rates and the use of new fishing opportunities. By providing a nightly measure of "proven stock" (Pearse and Walters 1992), these indices furnish a method for investigating biological and management factors that lead to the feedback effects of the decision rules (Claytor 2000). The adoption of a decision-rule approach, based on nightly abundance and exploitation rate indices, would produce a new paradigm for the management of herring spawning components.

Adoption of a decision-rule approach based on fishery acoustic indices would also alter the focus of assessment groups. The emphasis would shift from collecting data to describe the age structure of the population and to develop population models to one in which exploitation rates and their effects on the population are directly measured. The result would be an assessment process that is more transparent to industry. Future developments of this methodology will focus on these aspects of managing herring spawning components.

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PERSPECTIVE

Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes?

Anthony Ricciardi

Abstract: A widely cited hypothesis in ecology is that species-rich communities are less vulnerable to invasion than species-poor ones, owing to competition for limiting resources (the “biotic resistance” model). However, evidence for biotic resistance in aquatic ecosystems is equivocal. Contrary to the view that communities become more resistant to invasion as they accumulate species, the rate of invasion has increased over the past century in areas that have received frequent shipping traffic. Furthermore, introduced species may facilitate, rather than compete with, one another. A review of invasions in the Great Lakes indicates that direct positive (mutualistic and commensal) interactions among introduced species are more common than purely negative (competitive and amensal) interactions. In addition, many exploitative (e.g., predator–prey) interactions appear to be strongly asymmetric in benefiting one invading species at a negligible cost to another. These observations, combined with an increasing invasion rate in the Great Lakes, tentatively support the Simberloff – Von Holle “invasional meltdown” model. The model posits that ecosystems become more easily invaded as the cumulative number of species introductions increases, and that facilitative interactions can exacerbate the impact of invaders. It provides a theoretical argument for substantially reducing the rate of species introductions to the Great Lakes.

Résumé : Une hypothèse couramment citée en écologie veut que les communautés riches en espèces soient moins vulnérables aux invasions que les plus pauvres, à cause de la compétition pour les ressources limitantes (le modèle de la « résistance biotique »). Cependant, les preuves de l'existence d'une telle résistance biotiques dans les écosystèmes aquatiques sont équivoques. En contradiction avec l'opinion qui prétend que les communautés deviennent plus résistantes lorsqu'elles accumulent plus d'espèces, le taux d'invasion a augmenté au cours du siècle dernier dans les régions qui reçoivent un important trafic maritime. De plus, les espèces introduites peuvent même faciliter leur coexistence mutuelle plutôt qu'entrer en compétition. Une étude des invasions dans les Grands-Lacs révèle que les interactions directes positives (de mutualisme et de commensalisme) parmi les espèces introduites sont plus fréquentes que les interactions purement négatives (de compétition et d'amensalisme). De plus, plusieurs des interactions d'exploitation (e.g., de type prédateur-proie) semblent être fortement asymétriques en avantageant l'un des envahisseur à un coût négligeable pour l'autre. Ces observations ainsi que le taux croissant des invasions dans les Grands-Lacs semblent vouloir appuyer le modèle d' « effondrement des communautés à la suite des invasions » de Simberloff – Von Holle. Le modèle prédit que les écosystèmes deviennent de plus en plus faciles à envahir à mesure que le nombre cumulatif d'espèces introduites y augmente et que des actions facilitantes viennent exacerber l'impact des envahisseurs. Il s'agit donc d'un argument théorique pour limiter de façon importante le taux d'introduction d'espèces dans les Grands-Lacs.

[Traduit par la Rédaction]

Introduction

Biological invasion studies often focus on interactions between introduced species and native species. When interactions involving introduced species are considered, competition is typically emphasized (Moulton and Pimm 1983; Case 1990; Case and Bolger 1991). A widely cited hypothesis in invasion ecology is that species-rich communities are more resistant to invasion than species-poor ones because the former use limiting resources more completely and are also more likely to have competitors or predators that can exclude potential invaders (Elton 1958). This concept is the basis of the “biotic resistance model”, which predicts that successive invasions will cause a community to accumulate stronger com-

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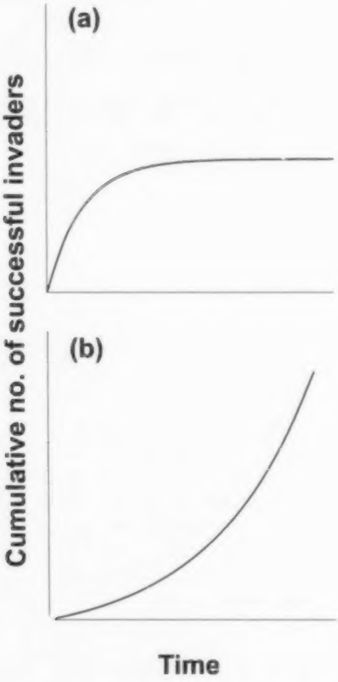
Fig. 1. Temporal trend in the cumulative number of successful invasions as predicted by (*a*) the biotic resistance model and (*b*) the invasional meltdown model.



petitors, more efficient predators, and well-defended prey (Moulton and Pimm 1983; Case 1990). Thus, the rate of establishment of new species in a community should become increasingly limited over time.

Contrary to the idea that areas become less vulnerable to invasion as they accumulate species, the rate of invasion is increasing in several aquatic ecosystems (e.g., Ribera and Boudouresque 1995; Leppäkoski and Olenin 2000). Even the most speciose aquatic ecosystems on the planet have been invaded multiple times (Kaufman 1992; Dumont 1998; Hall and Mills 2000), whereas some species-poor ecosystems have shown remarkable resistance to invasion (e.g., Baltz and Moyle 1993). An alternative to the biotic resistance model has been proposed by Simberloff and Von Holle (1999), who suggested that if communities are the outcome of a nonrandom sorting and adjustment process, then frequent species introductions may generate an increasing threat to community integrity in two ways: (*i*) as the cumulative number of attempted (including unsuccessful) introductions increases, populations of resident species are disrupted and the community thus becomes more easily invaded; and (*ii*) once established, some invaders alter habitat conditions in favor of other invaders, thereby creating a positive feedback system that accelerates the accumulation of nonindigenous species and their synergistic impacts. This defines the "invasional meltdown" model, which emphasizes facilitative (rather than antagonistic) interactions among introduced species (Fig. 1). Simberloff and Von Holle (1999) reviewed several cases, primarily from terrestrial ecosystems, where one invading organism facilitated another through mutualism, commensalism, or habitat modification (e.g., animals pollinating and dispersing plants). They cited European colonization of the New World as an example of a mutualistic process in which coevolved European animals, plants, and pathogens formed a "synergistic juggernaut" that facilitated their domination of native ecosystems. Furthermore, Simberloff and Von Holle (1999) suggested that such facilitation is a common phenomenon largely ignored by research that has focused on competitive interactions among invaders. Richardson et al. (2000) similarly concluded that facilitative interactions are widespread and important in accelerating the invasion of natural communities by plants. No such analysis has been done for aquatic invasions.

In this paper, I evaluate which of these models (biotic resistance or invasional meltdown) best explains the invasion history of the Great Lakes. First, I test two key components of the invasional meltdown model: (*i*) the premise that facilitative (positive) interactions are at least as common as negative interactions among introduced species; and (*ii*) the prediction of "an accelerating accumulation of introduced species" (Simberloff and Von Holle 1999), i.e., that the rate of invasion of the Great Lakes is increasing with time. Second, I examine evidence for biotic resistance in the aquatic ecology literature by reviewing studies that have explicitly tested the relationship between invasion success and the composition (diversity, trophic structure) of the resident community.

Methods

To test the first prediction of the invasional meltdown model, I reviewed all available published data for interactions among sympatric nonindigenous species in the Great Lakes. Literature sources were obtained primarily from references cited in Mills et al. (1993) and MacIsaac (1999), as well as from the electronic Aquatic Sciences and Fisheries Abstracts (ASFA) database (http://webspirs3.silverplatter.com). Species interactions were categorized as follows: mutualism, in which the interaction is beneficial to the survival and (or) population growth of both species; commensalism, in which one species benefits from the presence of another species that is unaffected by the interaction; exploitation, in which one species benefits at the expense of another (e.g., predation, parasitism); amensalism, in which one species is inhibited while the other is unaffected; and antagonism, which is defined here as any mutually detrimental interaction (e.g., resource competition, interference, allelopathy). Only direct pairwise interactions were tabulated. In cases where one invader had various positive and negative effects on another's abundance and survival, the net effect was estimated when information allowed at least a subjective ranking of the various effects; otherwise, the interaction was omitted. For less than 5% of the cases, when Great Lakes data were unavailable, an interaction was assumed to occur between sympatric species because it was observed between these species in another region.

The resulting dataset contained 101 pairwise interactions (Table 1). Obviously, this is a small sample of the actual set of interactions among Great Lakes invaders, because it includes only cases that are supported by empirical evidence, whereas the ecological interactions of most invaders are untested. Moreover, the dataset omits indirect interactions, such as indirect commensalisms in which one invader reduces the abundance or survival of another's enemies. Examples of this in the Great Lakes include the indirect enhancement of both the alewife *Alosa pseudoharengus* and the rainbow smelt *Osmerus mordax* owing to the suppression of native

Table 1. Ecological interactions among nonindigenous species established in the Great Lakes – St. Lawrence River system.

Species pairs	Reference
Mutualism (+/+) (3 cases)	
Bithynia tentaculata / *Dreissena polymorpha*	Ricciardi et al. 1997
Myriophyllum spicatum / *Dreissena polymorpha*	MacIsaac 1996; Skubinna et al. 1995
Potamogeton crispus / *Dreissena polymorpha*	MacIsaac 1996; Skubinna et al. 1995
Commensalism (+/0) (14 cases)	
Acineta nitocrae + / *Nitocra hibernica* 0	Grigorovich et al. 2001
Acineta nitocrae + / *Nitocra incerta* 0	Grigorovich et al. 2001
Bithynia tentaculata + / *Myriophyllum spicatum* 0	Vincent et al. 1981
Dugesia polychroa + / *Dreissena polymorpha* 0	Ricciardi et al. 1997; Ricciardi unpublished data
Dugesia polychroa + / *Dreissena bugensis* 0	Ricciardi et al. 1997; Ricciardi unpublished data
Echinogammarus ischnus + / *Dreissena polymorpha* 0	Stewart et al. 1998*a*, 1998*b*, 1998*c*
Echinogammarus ischnus + / *Dreissena bugensis* 0	Stewart et al. 1998*a*, 1998*b*, 1998*c*
Gammarus fasciatus + / *Dreissena polymorpha* 0	Ricciardi et al. 1997
Gammarus fasciatus + / *Dreissena bugensis* 0	Ricciardi et al. 1997; Dermott and Kerec 1997
Lophopodella carteri + / *Myriophyllum spicatum* 0	Wood 1989
Lophopodella carteri + / *Potamogeton crispus* 0	Wood 1989
Proterorhinus marmoratus + / *Potamogeton crispus* 0	Jude et al. 1995
Valvata piscinalis + / *Dreissena polymorpha* 0	Ricciardi et al. 1997
Valvata piscinalis + / *Dreissena bugensis* 0	Ricciardi et al. 1997
Exploitation (+/–) (73 cases)	
Herbivory	
Dreissena polymorpha + / *Stephanodiscus binderanus* –	Holland 1993; MacIsaac 1999
Dreissena polymorpha + / *Stephanodiscus subtilis* –	Holland 1993; MacIsaac 1999
Dreissena polymorpha + / *Skeletonema subsalum* –	Holland 1993; MacIsaac 1999
Dreissena polymorpha + / *Cyclotella cryptica* –	Holland 1993; MacIsaac 1999
Dreissena polymorpha + / *Cyclotella pseudostelligera* –	Holland 1993; MacIsaac 1999
Predator–prey relationships	
Alosa pseudoharengus + / *Osmerus mordax* –	Smith 1970
Alosa pseudoharengus + / *Eubosmina coregoni*–	Mills et al. 1995
Alosa pseudoharengus + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Alosa pseudoharengus + / *Cercopagis pengoi* –	E. Mills, personal communication
Alosa pseudoharengus + / *Dreissena polymorpha* –	Mills et al. 1995
Bythotrephes longimanus + / *Eubosmina coregoni* –	Grigorovich et al. 1998
Cordylophora caspia + / *Dreissena polymorpha* –	Molloy et al. 1997; Olenin and Leppakoski 1999
Cyprinus carpio + / *Dreissena polymorpha* –	Tucker et al. 1996
Cyprinus carpio + / *Dreissena bugensis* –	Ricciardi, unpublished data
Cyprinus carpio + / *Sphaerium corneum*–	Ricciardi, unpublished data
Cyprinus carpio + / *Bithynia tentaculata* –	Ricciardi, unpublished data
Gymnocephalus cernuus + / *Gammarus fasciatus* –	Fullerton et al. 1998
Gymnocephalus cernuus + / *Megacyclops viridis* –	Ogle et al. 1995
Morone americana + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Neogobius melanostomus + / *Dreissena polymorpha* –	Ray and Corkum 1997; Molloy et al. 1997
Neogobius melanostomus + / *Dreissena bugensis* –	Molloy et al. 1997
Neogobius melanostomus + / *Gammarus fasciatus* –	Ray and Corkum 1997; Jude et al. 1995
Neogobius melanostomus + / *Echinogammarus ischnus* –	Shorygin 1952
Oncorhynchus tshawytscha + / *Alosa pseudoharengus* –	Jude et al. 1987
Oncorhynchus tshawytscha + / *Osmerus mordax* –	Conner et al. 1993; Jude et al. 1987
Oncorhynchus tshawytscha + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Oncorhynchus gorbuscha + / *Alosa pseudoharengus* –	Smith 1970
Oncorhynchus gorbuscha + / *Osmerus mordax* –	Conner et al. 1993
Oncorhynchus gorbuscha + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Oncorhynchus kisutch + / *Alosa pseudoharengus* –	Jude et al. 1987
Oncorhynchus kisutch + / *Osmerus mordax* –	Conner et al. 1993; Jude et al. 1987
Oncorhynchus nerka + / *Alosa pseudoharengus* –	Smith 1970
Oncorhynchus nerka + / *Osmerus mordax* –	Conner et al. 1993
Oncorhynchus mykiss + / *Alosa pseudoharengus* –	Jude et al. 1987
Oncorhynchus mykiss + / *Osmerus mordax* –	Conner et al. 1993; Jude et al. 1987
Oncorhynchus mykiss + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Osmerus mordax + / *Eubosmina coregoni* –	Mills et al. 1995
Osmerus mordax + / *Dreissena polymorpha* –	Mills et al. 1995

Table 1 (*concluded*).

Species pairs	Reference
Osmerus mordax + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Proterorhinus marmoratus + / *Dreissena polymorpha* –	Molloy et al. 1997
Proterorhinus marmoratus + / *Dreissena bugensis* –	Molloy et al. 1997
Salmo trutta + / *Alosa pseudoharengus* –	Jude et al. 1987; Smith 1970
Salmo trutta + / *Osmerus mordax* –	Conner et al. 1993; Jude et al. 1987
Salmo trutta + / *Bythotrephes longimanus* –	Grigorovich et al. 1998
Parasite–host relationships	
Acanthostomum sp. + / *Gymnocephalus cernuus* –	Pronin et al. 1997*b*
Acentropus niveus + / *Myriophyllum spicatum* –	Mills et al. 1993
Acentropus niveus + / *Potamogeton crispus* –	Mills et al. 1993
Acentropus niveus + / *Trapa natans* –	Mills et al. 1993
Aeromonas salmonicida + / *Salmo trutta* –	Mills et al. 1993
Aeromonas salmonicida + / *Carassius auratus* –	Mills et al. 1993
Aeromonas salmonicida + / *Cyprinus carpio* –	Mills et al. 1993
Argulus japonicus + / *Carassius auratus* –	Mills et al. 1993
Dactylogyrus amphibothrium + / *Gymnocephalus cernuus* –	Cone et al. 1994
Dactylogyrus hemiamphibothrium + / *Gymnocephalus cernuus* –	United States Department of the Interior 1993
Glugea hertwigi + / *Osmerus mordax* –	Mills et al. 1993
Ichthyocotylurus pileatus + / *Neogobius melanostomus* –	Pronin et al. 1997*a*
Myxobolus cerebralis + / *Oncorhynchus tshawytscha* –	Mills et al. 1993
Myxobolus cerebralis + / *Oncorhynchus gorbuscha* –	Mills et al. 1993
Myxobolus cerebralis + / *Oncorhynchus kisutch* –	Mills et al. 1993
Myxobolus cerebralis + / *Oncorhynchus nerka* –	Mills et al. 1993
Myxobolus cerebralis + / *Oncorhynchus mykiss* –	Mills et al. 1993
Myxobolus cerebralis + / *Salmo trutta* –	Mills et al. 1993
Neascus brevicaudatus + / *Gymnocephalus cernuus* –	United States Department of the Interior 1993
Petromyzon marinus + / *Oncorhynchus tshawytscha* –	Pearce et al. 1980
Petromyzon marinus + / *Oncorhynchus mykiss* –	Berst and Wainio 1967
Petromyzon marinus + / *Oncorhynchus gorbuscha* –	Noltie 1987
Petromyzon marinus + / *Oncorhynchus kisutch* –	Pearce et al. 1980
Petromyzon marinus + / *Oncorhynchus nerka* –	Pearce et al. 1980
Petromyzon marinus + / *Cyprinus carpio* –	Christie and Kolenosky 1980
Sphaeromyxa sevastopoli + / *Neogobius melanostomus* –	Pronin et al. 1997*a*
Sphaeromyxa sevastopoli + / *Proterorhinus marmoratus* –	Pronin et al. 1997*a*
Trypanosoma acerinae + / *Gymnocephalus cernuus* –	United States Department of the Interior 1993
Overgrowth	
Lophopodella carteri + / *Dreissena polymorpha* –	Lauer et al. 1999
Amensalism (–/0) (4 cases)	
Habitat alteration	
Potamogeton crispus – / *Cyprinus carpio* 0	Lundholm and Simser 1999
Myriophyllum spicatum – / *Cyprinus carpio* 0	Lundholm and Simser 1999
Interference	
Elimia virginica – / *Bithynia tentaculata* 0	Harman 1968
Sphaerium corneum – / *Dreissena polymorpha* 0	Lauer and McComish 2001
Antagonism (–/–) (7 cases)	
Predation vs. allelopathy	
Oncorhynchus kisutch / *Alosa pseudoharengus*	Fitzsimons et al. 1999
Interspecific predation of larvae	
Proterorhinus marmoratus / *Neogobius melanostomus*	Jude et al. 1995
Resource competition	
Echinogammarus ischnus / *Gammarus fasciatus*	Dermott et al. 1998
Dreissena polymorpha / *Dreissena bugensis*	Mills et al. 1999
Sphaerium corneum / *Dreissena bugensis*	Dermott and Kerec 1997
Lythrum salicaria / *Typha angustifolia*	Mal et al. 1997
Oncorhynchus mykiss / *Salmo trutta*	Landergren 1999

Note: +, Enhanced survival or population growth; –, survival or population growth negatively affected; 0, unaffected.

predatory salmonids by introduced sea lamprey *Petromyzon marinus* during the 1940s and 1950s (Smith 1970; Christie 1974). Similarly, by preying heavily upon planktivores, introduced salmonids might have facilitated population expansion of large nonindigenous zooplankton such as *Bythotrephes longimanus* and *Cercopagis pengoi* (Jude et al. 1987; Conner et al. 1993). Indirect commensalism also occurs when one invader augments the food resources of another invader; for example, the zebra mussel *Dreissena polymorpha* increases the diversity and abundance of invertebrate prey for benthivorous fishes like the ruffe *Gymnocephalus cernuus*, whose growth rate may increase as a result (Thayer et al. 1997). In the invasional meltdown model, both direct and indirect facilitation accelerate the establishment of nonindigenous species through positive feedback loops (Fig. 2).

I tested the second prediction of the invasional meltdown model using linear regression analysis of data on the number of Great Lakes invasions documented between 1810 and 2000. Only those species known to be established (i.e., having formed reproducing populations) were included; therefore, some introduced species such as skipjack herring *Alosa chrysochloris* (Fago 1993) and grass carp *Ctenopharyngodon idella* (Crossman et al. 1987) were omitted. My review yielded a total of 162 invaders (see Appendix A for species additional to those listed by Mills et al. 1993).

Finally, to assess evidence of biotic resistance in aquatic systems, I searched the ASFA database for published studies that contained the following combinations of key words: (INVAD* or INTRODUCED or NONINDIGENOUS or ALIEN or EXOTIC) and RESISTANCE. The ASFA database contained studies published from 1978 to 2000, inclusive. My intention was to determine whether negative relationships between invasion success and species diversity within a community have been demonstrated for freshwater, brackish-water, or marine communities.

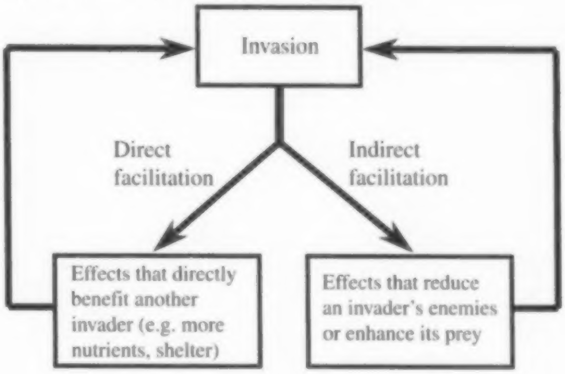
Results and discussion

Facilitative versus antagonistic interactions among invaders in the Great Lakes

Contrary to the biotic resistance model, which assumes the dominance of negative interactions among introduced species, the number of cases of direct positive interactions (3 mutualisms and 14 commensalisms) exceeds the number of cases of purely negative interactions (4 amensalisms and 7 antagonistic interactions) (Table 1). All mutualisms and commensalisms listed here are facultative. About 72% (73/101) of interactions in the dataset are exploitative, being mostly predator–prey and parasite–host relationships. These cannot be interpreted as purely negative interactions, because one invader clearly benefits from the other's presence. Moreover, in many cases, the interaction is probably strongly asymmetric such that the prey and (or) host population is only weakly affected because of its high recruitment rate or because of the relatively low abundance of the predator or parasite, i.e., prey abundance may control predator abundance, but not vice versa. These interactions appear to have such a negligible cost to the host or prey species that they could be considered commensal (examples include the moth *Acentropus niveus* and its plant hosts; some molluscivorous fishes and their zebra mussel prey; planktivorous fishes and zebra mussel larvae; Mills et al. 1993; Molloy et al. 1997).

In about one third (25/73) of the cases of exploitation, the newcomer benefited from the presence of a previously established invader. For example, the presence of abundant and widespread zebra mussel populations likely facilitated the establishment and spread of the round goby *Neogobius melanostomus*, one of the mussel's principal predators in the Ponto–Caspian (Black and Caspian Seas) region (Shorygin 1952; Ray and Corkum 1997). Similarly, the prior establishment of abundant zooplanktonic prey in the form of zebra mussel larvae and the cladoceran *Eubosmina coregoni* may have aided the invasion of blueback herring, *Alosa aestivalis*, in Lake Ontario (Molloy et al. 1997; MacNeill 1998).

Fig. 2. Positive feedback mechanisms of the invasional meltdown model. An example of direct facilitation is the provision of biodeposits and shelter by an introduced mussel for an introduced detritivore. An example of indirect facilitation is the reduction of piscivores by an introduced parasite (e.g., sea lamprey), paving the way for invasion by a planktivore (e.g., alewife).


Invasion
Direct facilitation
Indirect facilitation
Effects that directly benefit another invader (e.g. more nutrients, shelter)
Effects that reduce an invader's enemies or enhance its prey

Evidence of an invasional meltdown in the Great Lakes

The invasional meltdown model is supported by the increasing rate of invasion in the Great Lakes over the past two centuries (Fig. 3). Among the 162 nonindigenous species in the system, 40 were recorded during the first half of the 20th century and 76 during the latter half of the 20th century. Since 1970, on average, there has been one invader recorded every eight months. The number of species established per decade has increased with time, and none has subsequently become extirpated. The trend in the cumulative number of successful invasions over the past two centuries is best described by a quadratic function (Fig. 3), which explains 4% more variance than a simple linear function. This trend might partially reflect recent awareness and monitoring efforts to locate invaders; however, much of the taxonomic and survey work on Great Lakes biota was carried out several decades ago. Undoubtedly, some invasions have gone unnoticed, and there are several species of cryptogenic invertebrates (species of uncertain origin but assumed to be holarctic or cosmopolitan) that may have been introduced in the distant past (Mills et al. 1993).

Another potential explanation for the increasing invasion rate is the strong positive relationship between the number of nonindigenous species established per decade and shipping activity (net tonnage of cargo ships) in the Great Lakes (Fig. 4). Shipping activity explains 62% of variation in the invasion rate, despite the fact that nearly half of all invasions that occurred over the past century are attributable to other vectors. Shipping still accounts for more invasions than any other single vector, and its influence has grown in recent decades: 77% (36 of 47) of invasions since 1970 were likely caused by transoceanic shipping (see Mills et al. 1993 and references in Appendix A). Surprisingly, the relationship obtained using data for all invaders is stronger than the one obtained using only species assumed to have been transported

Fig. 3. Changes in the numbers of nonindigenous species established in the Great Lakes as a function of time (decades) in which the species was discovered or presumed introduced. (*a*) Number of invaders per decade ($y = 0.79x$, $r^2_{\text{adj}} = 0.71$, $P < 0.0001$). (*b*) Cumulative number of invaders over time ($y = 1.50x + 0.37x^2$, $r^2_{\text{adj}} = 0.997$, $P < 0.0001$). Least-squares regression lines are shown. Data are from Mills et al. (1993) and references are given in Appendix A.

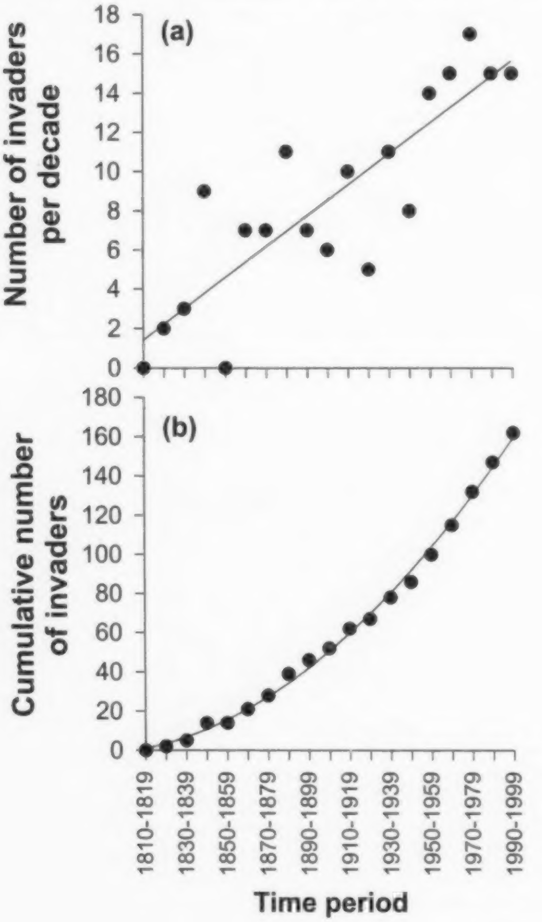
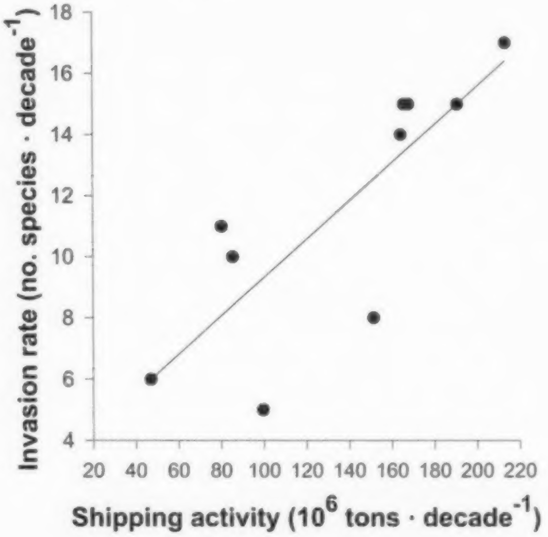


Fig. 4. Invasion rate versus shipping activity in the Great Lakes from 1900 to 1999 ($y = 0.062x$, $r^2_{\text{adj}} = 0.62$, $P < 0.004$). Shipping activity is measured in net tonnage (1 ton (Imperial) = 0.9842 t) of cargo ships (both foreign and domestic vessels) averaged over all years within each decade; data are from Lake Carriers' Association (1999).

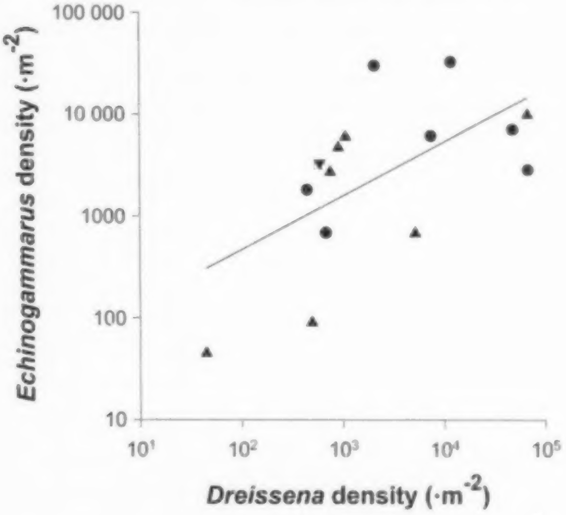


with ships, either in ballast water or as fouling organisms on ship hulls ($r^2 = 0.43$, $P < 0.023$). The stronger correlation may be due, in part, to factors coincident with increasing shipping activity, such as changing trade patterns that have resulted in an increased diversity of donor regions linked to the Great Lakes. Alternatively, invasions may be succeeding more easily now than ever before because of facilitation among invaders. A positive feedback cycle of invasion should yield a stronger correlation involving all invaders rather than only a subset of species associated with a particular vector. Unfortunately, it is not possible to clearly separate the effects of facilitation and inoculation pressure (e.g., caused by to increased ship traffic) on the rate of invasion.

Although shipping activity likely contributes to the increased accumulation of invaders in the Great Lakes, the number of invaders recorded in the 1990s (15 species) does not differ from previous decades (15 in the 1980s, 17 in the 1970s, 15 in the 1960s) despite regulations requiring inbound ships to exchange their freshwater–estuarine ballast with oceanic water. Voluntary ballast water exchange guidelines were initiated by the Canadian government in 1989, and approximately 90% of ships complied with the procedure even before it became mandatory by U.S. regulation in 1993 (Locke et al. 1993). In theory, mid-oceanic ballast water exchange should reduce the risk of invasion because freshwater organisms would be purged from the ballast tanks or killed by incoming seawater, and be replaced by marine organisms that could not survive if released into the Great Lakes. However, owing to the position of the pump intake, it is impossible to empty ballast tanks completely, so oceanic salinities are rarely achieved (Locke et al. 1993). Therefore, ballast water exchange may not prevent invasions by species with broad salinity tolerance and by species with resistant resting stages that are unlikely to be removed by exchange nor killed by contact with seawater.

Indeed, since the early 1990s, ships have continued to introduce species including the amphipod *Echinogammarus ischnus*, the copepod *Schizopera borutzkyi*, and the waterflea *Cercopagis pengoi* (Witt et al. 1997; MacIsaac et al. 1999; Horvath et al. 2001). A living specimen of another amphipod, *Corophium mucronatum*, was collected in Lake St. Clair in 1997, but the species has apparently not become established (Grigorovich and MacIsaac 1999). Other failed species introductions during the 1990s include nonreproducing European flounder (*Platichthys flesus*) and Chinese mitten crab (*Eriocheir sinensis*) (E.L. Mills, Cornell University, Biological Field Station, Bridgeport, N.Y., personal communication). Thus, during the 1990s there was a

Fig. 5. Density of the Ponto–Caspian amphipod *Echinogammarus ischnus* as a function of *Dreissena* mussel density in the Great Lakes (least-squares regression of log-transformed data, $y = 1.61 + 0.53x$, $r^2_{adj} = 0.32$, $P < 0.017$). Data are from Stewart et al. (1998*a*, 1998*b*, 1998*c*) and R. Dermott, Department of Fisheries and Oceans, Burlington, Ont. (personal communication). ●, Western Lake Erie; ▲, eastern Lake Erie; ▼, St. Clair River.



strong shift toward introductions of euryhaline animal species, most of which originate from Ponto–Caspian basins.

The recent influx of Ponto–Caspian invaders is attributable to strong invasion corridors (i.e., transportation vectors and dispersal pathways) linking the Great Lakes with Eurasia (Ricciardi and MacIsaac 2000). Invasion corridors shunt large numbers of propagules from particular donor pools into new regions, thereby assembling co-evolved alliances and foreign food webs in the recipient habitat like pieces of an ecological jigsaw puzzle. For example, sequential invasions by Ponto–Caspian species have completed the parasitic life cycle of the trematode *Bucephalus polymorphus* in Western Europe. The introductions of its first intermediate host (the zebra mussel) and its definitive host (the pikeperch *Stizostedion lucioperca*) allowed the trematode to spread into inland waters and cause high mortality in local populations of cyprinid fishes, which act as secondary intermediate hosts (Combes and Le Brun 1990). In the Great Lakes, facultative host–parasite complexes of nonindigenous species have become established, including parasites of introduced gobies (*N. melanostomus* and *Proterorhinus marmoratus*) and of the ruffe *Gymnocephalus cernuus* (Pronin et al. 1997*a*, 1997*b*; Cone et al. 1994). These parasites were probably introduced simultaneously with their hosts.

Ponto–Caspian invaders have also been facilitated by habitat alterations caused by dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*). *Dreissena* spp. are involved in all three cases of mutualism and 8 of the 14 cases of commensalism (e.g., Fig. 5). Food (in the form of fecal deposits) and habitat complexity produced by mussel beds have stimulated a 20-fold increase in the biomass of the amphipod *E. ischnus* in Lake Erie (Stewart et al. 1998*a*). Mussel beds might also offer amphipods a refuge from fish predation (Gonzalez and Downing 1999). In addition, by colonizing fine sediments in western Lake Erie, *Dreissena* has facilitated the expansion of *Echinogammarus* into habitats that were previously unsuitable (Bially and MacIsaac 2000). Thus, the introduced mussels stimulate a prey resource for juvenile round gobies, which feed predominantly on gammarid amphipods in their native range, whereas adult gobies feed preferentially on the mussels themselves (Shorygin 1952; Ray and Corkum 1997). Another beneficiary is the Ponto–Caspian hydroid *Cordylophora caspia*, which consumes zebra mussel larvae and uses mussel shells as substrate (Olenin and Leppäkoski 1999). After having been relatively inconspicuous in the Great Lakes for decades, *Cordylophora* has been observed growing luxuriantly on mussel beds in Lake Michigan in recent years (T. Lauer, Ball State University, Muncie, Ind., personal communication). In Lake St. Clair and Saginaw Bay, Lake Huron, zebra mussel filtration has substantially increased water transparency, thereby stimulating the growth of exotic and native macrophytes (Skubinna et al. 1995; MacIsaac 1996), which in turn provide substrate for settling juvenile mussels and facilitate their dispersal (Horvath and Lamberti 1997). In the St. Lawrence River, the European faucet snail, *Bithynia tentaculata*, has tripled its abundance in association with the growth of dense mussel populations, whose shells support rich microflora and provide the small snail with increased grazing area (Ricciardi et al. 1997) as well as potential refuge from large predators (Stewart et al. 1999). In return, the grazing activities of the snail reduce fouling sponge colonies that can overgrow and smother mussels (Ricciardi et al. 1995; A. Ricciardi, unpublished data).

If co-evolution reduces the intensity of interspecific interactions (Case and Bolger 1991), then successive introductions of species originating from the same endemic region may not be limited by competition, contrary to predictions of community assembly models. In addition to the Great Lakes, facilitation among invaders and reassembly of co-evolved food webs have also been observed in the Baltic Sea, where most of the invaders discovered since 1990 are of Ponto–Caspian origin (Leppäkoski and Olenin 2000). However, positive interactions in the Great Lakes and the Baltic Sea often involve species that share no evolutionary history. In the Great Lakes, for example, the Asian bryozoan *Lophopodella carteri* commonly uses Eurasian macrophytes as substrate (Wood 1989). The amphipod *Gammarus fasciatus*, native to the Atlantic region of North America, thrives in Ponto–Caspian mussel beds (Ricciardi et al. 1997). In the Baltic Sea, shells of the American barnacle *Balanus improvisus* provide shelter for Ponto–Caspian amphipods (Olenin and Leppäkoski 1999). *Balanus* itself uses zebra mussels as substrate (Olenin and Leppäkoski 1999), and may benefit from direct exposure to mussel filtration currents as it does in its commensal relationship with *Mytilus* (Laihonen and Furman 1986).

Is the biotic resistance hypothesis generally valid for aquatic communities?

Elton's (1958) proposition that species-rich communities are more resistant to invaders is supported by mathematical models and some field studies (e.g., Moulton and Pimm

1983; Case 1990; Reusch 1998). The evidence is equivocal, however. As noted by Levine and D'Antonio (1999), mathematical models are based on communities that are at equilibrium prior to invasion, whereas many natural communities appear to be unsaturated or successional (Cornell 1999). Various studies have found the relationship between invasion success and community diversity to be negative, positive, or insignificant (reviewed by Levine and D'Antonio 1999). Negative relationships, when observed, occur at small spatial scales (e.g., ~1 m^2 or less). Positive relationships tend to occur at regional scales (thousands of square metres) and suggest that the same environmental properties that support a rich diversity of native species may also support a rich diversity of introduced species (Levine and D'Antonio 1999).

Biotic resistance is hypothesized to occur at two stages of invasion: at the establishment stage and, if establishment is successful, during subsequent population growth, when the abundance of the invader (and thus its community-wide impact) is limited by resident species richness (Elton 1958; Case 1990; Shurin 2000). I have found only four documented studies (published before 2001) that have explicitly tested biotic resistance to establishment in aquatic communities; two of these support the biotic resistance model. After inoculating fishless ponds with nonindigenous zooplankton, Shurin (2000) found that both the proportion of successful introductions and the biomass of introduced species was negatively correlated with native species richness. In the second study, using experimental communities of sessile marine invertebrates, Stachowicz et al. (1999) reported that survivorship among introduced species declined with increasing community richness, apparently because of competition for space. However, they tested communities composed of only 0 to 4 epifaunal species. Experiments with small communities may have little predictive power if the relationship between invasibility and species richness is asymptotic over the range of community sizes commonly found in nature.

The two remaining studies do not support the biotic resistance model. In an analysis of 125 North American drainages, Gido and Brown (1999) found a weak negative correlation between the number of introduced fish species and the number of native fish species historically present in a drainage. However, their random simulations showed that this pattern was due to a statistical artifact: drainages with low native diversity may receive introductions from a greater pool of potential invaders in neighboring drainages. Furthermore, not all drainages with low native diversity were colonized by large numbers of introduced fishes; relatively fewer invasions occurred in drainages situated in extreme northern environments and in drainages whose river flow was less regulated.

Contrary to the notion that species-poor communities are highly vulnerable to invasion, Baltz and Moyle (1993) observed that a depauperate fish assemblage in an unregulated stream resisted invasion, despite inoculation pressure from several nonindigenous fishes inhabiting other parts of the drainage basin. Their analysis suggested that abiotic factors and the presence of native predators were more important than interspecific competition in maintaining community integrity. Similarly, an abundance of large piscivores may have been responsible for preventing the expansion of the alewife from the St. Lawrence River into the Great Lakes, prior to the construction of the Erie Canal (Smith 1970). However, predator diversity does not appear to be a good predictor of invasibility. Although European studies suggest that fish predation may exclude the waterflea *Bythotrephes longimanus* (=*cederstroemi*) from lakes within its natural range (Grigorovich et al. 1998), selective predation by planktivorous fishes did not prevent *Bythotrephes* or another waterflea, *Cercopagis pengoi*, from becoming established in Lake Ontario (MacIsaac et al. 1999), which has the highest degree of planktivory among the Great Lakes (Rand et al. 1995). Both species were established in Lake Ontario prior to invading other Great Lakes. *Bythotrephes* also became established in Harp Lake, Ontario, despite the presence of (*i*) a rich, stable zooplankton community, and (*ii*) intense planktivory from lake herring *Coregonus artedii* and from a diverse assemblage of macroinvertebrate predators including *Leptodora kindtii*, opossum shrimp *Mysis relicta*, phantom midge *Chaoborus punctipennis*, and the jellyfish *Craspedacusta sowerbyi* (Yan and Pawson 1997; Coulas et al. 1998). Similarly, rainbow smelt have colonized a wide variety of inland lakes possessing sparse to rich communities of predators (Evans and Loftus 1987). There are also several examples of marine algae that have become established in the presence of a diverse assemblage of invertebrate grazers (Trowbridge 1995). In fact, there are theoretical reasons for predicting a positive relationship between invasibility and predator diversity. Pimm (1989) hypothesized that communities having a large variety of predators might be more vulnerable to invasion because predators reduce interspecific competition at lower trophic levels. Interference competition among predator species may also reduce pressure on introduced prey organisms (Soluk 1993).

Evolved versus contrived community diversity

Are rich communities of co-evolved fauna more resistant to invasion? Perhaps so, but numerous examples demonstrate the vulnerability of such communities. Lake Victoria had one of the richest endemic fish communities on the planet, but was devastated by a single invader, Nile perch *Lates niloticus*, which encountered neither predation nor competition from native fishes (Kaufman 1992). Rich, co-evolved communities in the Caspian Sea, Lake Baikal, Lake Biwa, and Lake Titicaca have also been invaded multiple times (Dumont 1998; Hall and Mills 2000). Mississippi River fish communities are among the most speciose of all temperate rivers, but have been invaded by several nonindigenous fishes including common carp *Cyprinus carpio*, goldfish *Carassius auratus*, grass carp *Ctenopharyngodon idella*, striped bass *Morone saxatilis*, rainbow smelt *Osmerus mordax*, rainbow trout *Oncorhynchus mykiss*, and white catfish *Ictaluris catus* (Burr and Page 1986). The zebra mussel has become established at high densities throughout the Mississippi River basin, which contains the world's richest endemic assemblage of freshwater mussels (Ricciardi et al. 1998). However, Lake Victoria cichlids and Mississippi River mussels are rapidly evolving species flocks that developed in the absence of predators like the Nile perch and biofoulers like the zebra mussel, and thus were ecologically naïve to their effects.

The hypothesis that a community is less likely to be invaded when introduced species encounter diverse competitors is suggested by terrestrial field studies (Moulton and Pimm 1983; Case and Bolger 1991), but is difficult to test rigorously because of the scarcity of data on failed introductions. Nevertheless, numerous counterexamples suggest that this hypothesis is not broadly valid in aquatic systems. The presence of ecologically or taxonomically similar native species has not prevented the establishment of several nonindigenous algae in coastal marine communities worldwide (Trowbridge 1995; Ribera and Boudouresque 1995). Following the opening of a major shipping canal between the Don and Volga rivers, the Caspian Sea was invaded by several Mediterranean invertebrates, including a mussel *Mytilaster lineatus* that caused the extinction of a confamilial endemic mussel *Dreissena caspia* (Dumont 1998). *Echinogammarus ischnus*, a deposit-feeding amphipod that inhabits zebra mussel beds in Europe (Köhn and Waterstraat 1990), is replacing the previously dominant amphipod *G. fasciatus* from mussel-covered substrate in Lake Erie, Lake Ontario, and the upper St. Lawrence River (Dermott et al. 1998; A. Ricciardi, unpublished data). Moyle (1986) noted that North American cold-water lakes and streams often contain several species of salmonids not co-evolved; brook trout *Salvelinus fontinalis*, rainbow trout *O. mykiss*, and brown trout *Salmo trutta* coexist in many streams because of their differing temperature preferences and spawning times. Similarly, numerous cyprinid minnows have become established in North American lakes and rivers where rich communities of native cyprinids were already present (Moyle 1986).

Unsuccessful introductions are less likely to be reported, or even noticed, than successful ones; this bias could obscure evidence of communities that have resisted invasion. However, where failed introductions are documented, they are often attributable to an invader's inability to adapt to abiotic conditions. For example, the Chinese mitten crab *E. sinensis* and the European flounder *P. flesus* have been frequently introduced to the Great Lakes in ship ballast water over the past few decades (Emery and Teleki 1978; MacIsaac 1999), but the environment is not saline enough for their successful reproduction. Reproducing populations of the Asiatic clam *Corbicula fluminea* in western Lake Erie, southern Lake Michigan, and the St. Clair River are restricted to waters artificially heated by discharge from power plants (Mills et al. 1993); *Corbicula*'s absence from most of the Great Lakes is better explained by its narrow thermal tolerance rather than biotic factors. Other examples are provided by introduced fishes, which often fail to invade rivers with extreme natural flow regimes (Meffe 1991; Baltz and Moyle 1993), but may do so when river flow is stabilized by impoundment (Moyle 1986; Gido and Brown 1999).

Some studies support the hypothesis that the abundance of an invading species is limited by resident species richness. Shurin (2000) found that introduced zooplankton achieved higher biomasses in enclosures where the resident species biomass was artificially reduced; therefore, he concluded that invaders were suppressed by strong interactions with resident species. Using fish exclusion cages, Robinson and Wellborn (1988) found a 29-fold reduction in the density of *C. fluminea* in the presence of a diverse assemblage of molluscivores within a Texas reservoir. Conversely, only a small number of native molluscivores were necessary to limit the abundance of the introduced marine mussel *Musculista senhousia* in a southern California bay; 65% of mussel mortality was caused by one species of muricid snail (Reusch 1998). Thus, a single predator or parasite species might be sufficient to prevent an introduced species from becoming dominant. Conversely, even when an introduced species encounters predation pressure from a diverse assemblage of consumers it may not necessarily be prevented from becoming dominant, as demonstrated by both the *Bythotrephes longimanus* and the round goby, *N. melanostomus*, invasions in the Great Lakes (Jude et al. 1995; Yan and Pawson 1997). Clearly, statistical syntheses are needed to test the generality of biotic resistance in aquatic communities.

Conclusion

The invasion history of the Great Lakes is explained better by the invasional meltdown model than by the biotic resistance model. Mutualistic, commensal, and asymmetric exploitative interactions facilitate the survival and population growth of many Great Lakes invaders. Direct positive interactions are more common than negative ones, and often involve species that have no co-evolutionary history. The recent influx of Ponto–Caspian animals suggests that Great Lakes communities remain highly susceptible to invasion. Further colonization by Ponto–Caspian species is likely because current ballast water controls apparently cannot prevent the delivery of euryhaline organisms; Ricciardi and Rasmussen (1998) identified 17 additional Ponto–Caspian species that are probable future invaders of the Great Lakes based on their invasion histories in Europe and their likelihood of surviving overseas transport in ship ballast tanks.

There is no compelling evidence that rich aquatic assemblages resist invasion when organisms are introduced repeatedly. If abiotic conditions are suitable and dispersal opportunities exist, aquatic species will likely invade regardless of the composition of the resident community. If biotic resistance to establishment exists only at a low frequency of attempted introductions, then invasional meltdown might be a threshold effect of inoculation pressure, which is high in aquatic systems subject to frequent ballast water discharge. Moreover, biotic resistance appears more likely to operate only at small scales (Levine and D'Antonio 1999), while invasional meltdown is hypothesized to operate at multiple scales—from communities to ecosystems (Simberloff and Von Holle 1999).

The invasional meltdown model has important implications for ecosystem management and biodiversity. If an increased frequency of introduction causes an ecosystem to be more susceptible to invasion, then efforts to severely reduce the rate of invasion are warranted. This refutes the criticism that resources allocated toward prevention are wasted if some future invasions are inevitable. Furthermore, because the impact of an invader is a function of its abundance, and because its abundance may be enhanced by facilitative interactions with other invaders, frequent introductions may result in synergistic impacts (Simberloff and Von Holle 1999). Complex combinations of interactions may render these impacts unpredictable. Finally, although invasional meltdown may increase local diversity through the accumulation of introduced species, the continuing replacement of endemic species by widespread invaders will inevitably reduce diversity among habitats and among regions (e.g., Rahel 2000). Invasional meltdown may accelerate the homogenization of ecosystems.

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Appendix A. Nonindigenous species in the Great Lakes basin not listed by Mills et al. (1993).

Species	Common name	Endemic region	Date	Reference
Algae				
Thalassiosira baltica	Diatom	Europe	1988*	Edlund et al. 2000
Myxozoans				
Sphaeromyxa sevastopoli	Mixosporidian	Black Sea	1994	Pronin et al. 1997*a*
Protozoans				
Acineta nitocrae	Suctorian	Eurasia	1970s*	Grigorovich et al. 2001
Trypanosoma acerinae	Flagellate	Black Sea	1980s*	United States Department of the Interior 1993
Monogeneans				
Dactylogyrus amphibothrium	Monogenetic fluke	Eurasia	1980s*	Cone et al. 1994

Appendix A (*concluded*).

Species	Common name	Endemic region	Date	Reference
Dactylogyrus hemiamphibothrium	Monogenetic fluke	Eurasia	1980s*	United States Department of the Interior 1993
Trematodes				
Neascus brevicaudatus	Digenean fluke	Eurasia	1980s*	United States Department of the Interior 1993
Acanthostomum sp.	Digenean fluke	Unknown	1992	Pronin et al. 1997*b*
Ichthyocotylurus pileatus	Digenean fluke	Black Sea	1994	Pronin et al. 1997*a*
Mollusks				
Pisidium supinum	Humpback pea clam	Europe	1959	MacIsaac 1999
Pisidium henslowanum	Henslow's pea clam	Eurasia	<1916	MacIsaac 1999
Potamopyrgus antipodarum	Mud snail	New Zealand	1991	Zaranko et al. 1997
Crustaceans				
Nitocra hibernica	Harpacticoid copepod	Eurasia	1973	Hudson et al. 1998
Nitocra incerta	Harpacticoid copepod	Black Sea	1999	Grigorovich et al. 2001
Megacyclops viridis	Cyclopoid copepod	Europe	1994	Hudson et al. 1998; Ogle et al. 1995
Echinogammarus ischnus	Amphipod	Black Sea	1995	Witt et al. 1997
Bosmina maritima	Cladoceran	Eurasia	<1980s*	De Melo and Hebert 1994
Heteropsyllus cf. *nunni*.	Harpacticoid copepod	unknown	1990s*	Horvath et al. 2001
Schizopera borutzkyi	Harpacticoid copepod	Black Sea	1998	Horvath et al. 2001
Cercopagis pengoi	Fish-hook waterflea	Black Sea	1998	MacIsaac et al. 1999
Daphnia lumholtzi	Waterflea	Africa, Asia	1999	Muzinic 2000
Ectoproct bryozoans				
Lophopodella carteri	Bryozoan	Asia	1934	Ricciardi and Reiswig 1994
Fishes				
Alosa aestivalis	Blueback herring	Atlantic North America	1995	MacNeill 1998

Note: Date refers to year of first collection. Assumed date of introduction is indicated by an asterisk.

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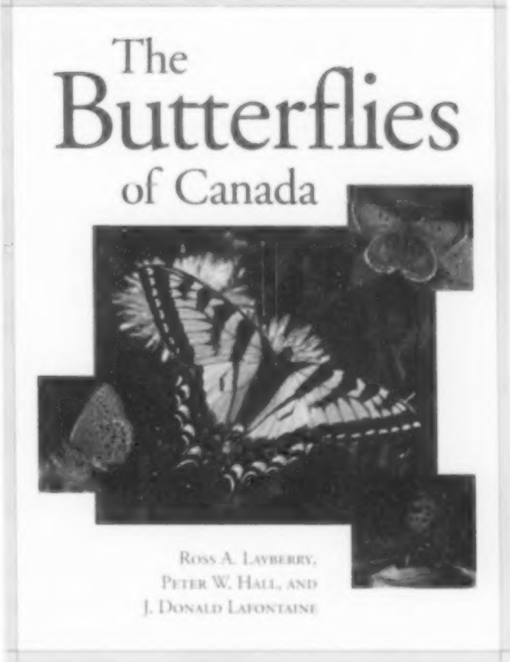

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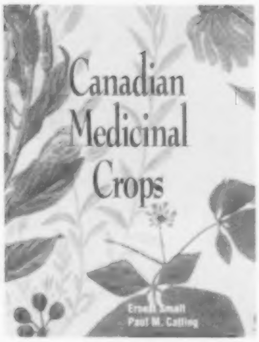

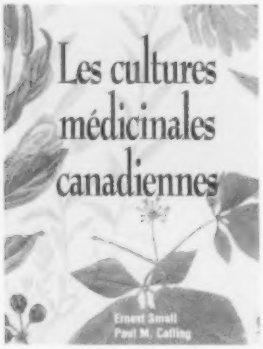

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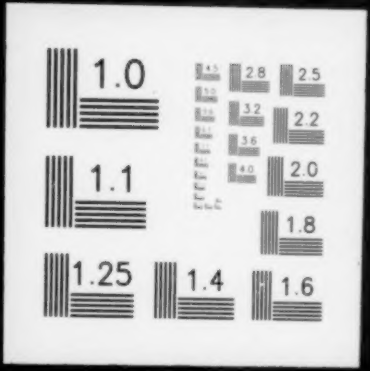
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